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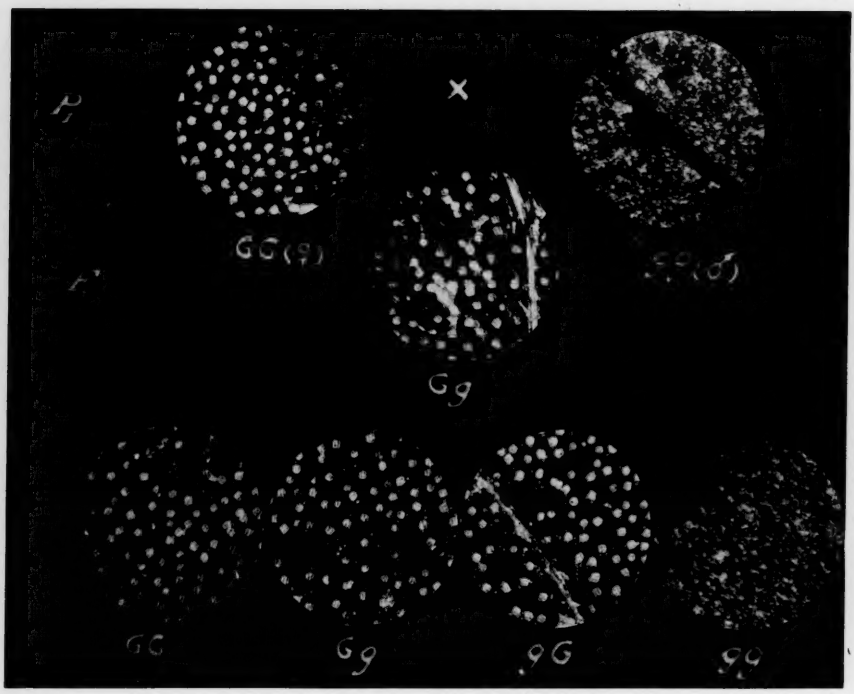

INHERITANCE OF LEAF GLANDS
(SEE PAGE 135)

Gaga Sweet Corn

An Albino Mud Puppy

Sex Uncontrolled in Rabbits

Species Hybrids in Lady Beetles

A Pedigree of Complete "Smell Blindness"

VOLUME 36 MAY, 1945 NUMBER 5

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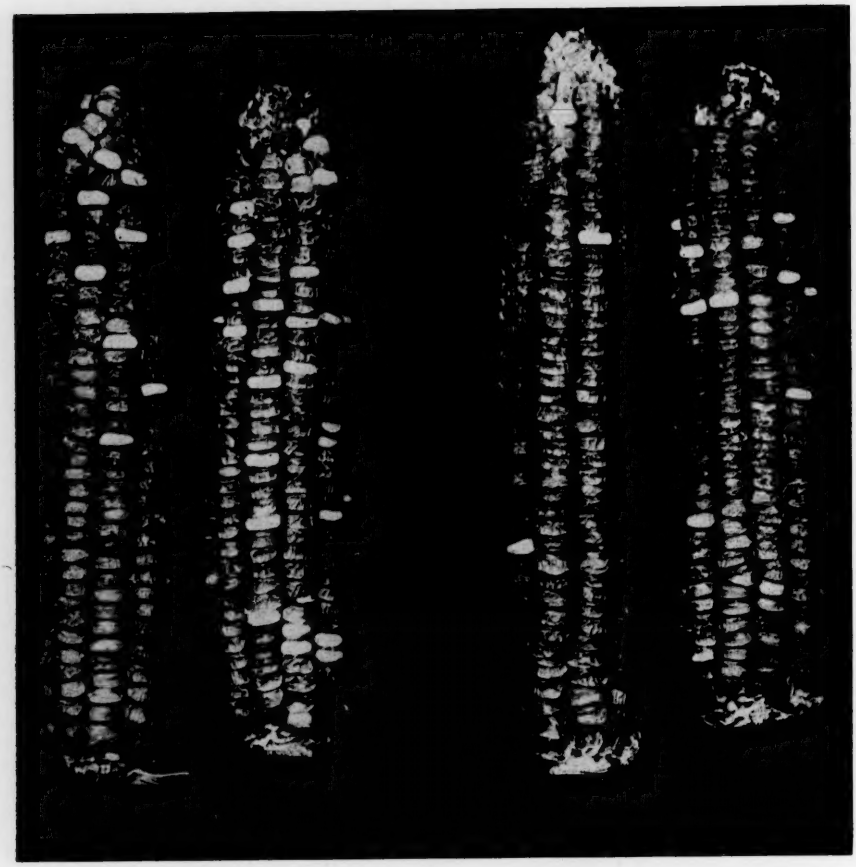


"RESISTANCE" TO CONTAMINATION

Figure 1

The *Ga* gene gives *Ga* pollen grains an advantage over *ga* pollen grains in achieving fertilization. (The symbol *Ga* signifies that this is a "gamete gene" causing "selective fertilization.") This photograph shows the effect of *Ga* in reducing contamination by wind-borne *ga* pollen from field corn. The starchy field corn grains show up whiter than the sugary sweet corn grains. At the left are two ears of Golden Cross Bantam of the genotype *ga ga*. The other two ears are slightly modified Golden Cross Bantam of the genotype *Ga ga*. The first and third ears are from the test here described. The second and fourth ears are from a preliminary test in which contaminations were more numerous. At least three-fourths of the usual contaminations can be prevented by introducing *Ga* into sweet corn.

THE *Ga* GENE AS A MEANS OF REDUCING CONTAMINATION OF SWEET CORN

H. S. PERRY

Department of Botany, Duke University

CONTAMINATION of sweet corn by wind-borne pollen from field corn is a common occurrence. On ripe ears the resulting smooth starchy grains differ conspicuously from the wrinkled sugary grains of the sweet corn. At the stage when sweet corn is normally harvested, these starchy grains differ little or not at all from the sugary grains in appearance. They do, however, differ in flavor and in texture and their presence impairs the quality of the product. The author has previously outlined a scheme[3] to utilize the gene *Ga* in making sweet corn less susceptible to such contamination and a test of its effectiveness has now been made.

The known effects of *Ga* have been described by Mangelsdorf and Jones[2] and by Emerson.[1] This gene gives pollen grains which carry it an advantage in competition with pollen grains carrying its recessive allele, *ga*, in the processes leading to fertilization within pistils which themselves carry *Ga*. Emerson concluded from tests made by himself and by others that when the two sorts of pollen are applied together in equal quantities by hand, fertilization is accomplished by *ga* microgametes only about four times in a hundred as a maximum. The percentage ranges downward almost to zero as a minimum.

Most, if not all, varieties of sweet corn and field corn are of the genotype, *ga ga*. The introduction of *Ga* into sweet corn should therefore give its own pollen an advantage in competition with field corn pollen and so reduce the frequency of contamination.

Material and Method

The deservedly popular hybrid, Golden Cross Bantam, was used as experimental material. Seed stocks of the parents of this hybrid were provided through the kindness of its originator, Mr. Glenn M. Smith of the United States Department of Agriculture.

Ga was introduced into one of these parents, Purdue 51, by a cross with a stock carrying *Ga* and *Su* (starchy endosperm) and by a series of four backcrosses to Purdue 51. The *Su* gene because of linkage provided a convenient means of testing for the presence of *Ga*. Further breeding and testing yielded segregates of the known genotype *su su Ga Ga*. These plants were "31/32" Purdue 51.

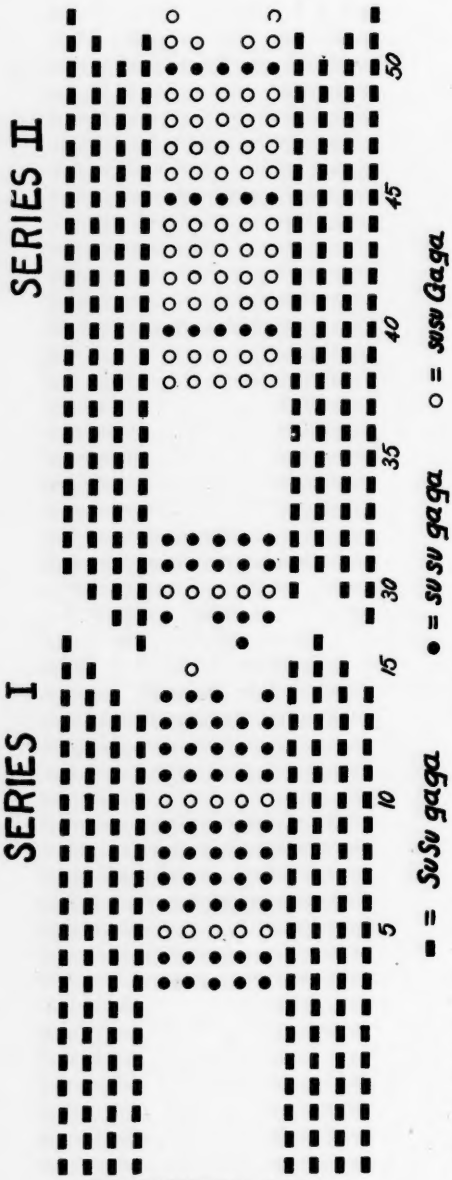
Such plants were substituted for Purdue 51 in crosses to produce modified Golden Cross Bantam hybrids. These hybrids are "63/64" Golden Cross Bantam and are similar to the original in yield, habit of growth, and quality. They are, however, heterozygous for *Ga*.

Testing Procedure

To test the effectiveness of *Ga* as a means of reducing contamination, the *Ga ga* hybrids were compared with Golden Cross Bantam as a control under conditions of natural pollination and free exposure to contamination. Portions of the experimental layout are diagramed in Figure 2.

The whole layout occupied an area 26 feet wide and 170 feet long. Four rows of starchy "roasting-ear" corn (*ga ga Su Su*) along each side were timed in planting to insure a continuous source of contaminating pollen throughout the flowering period of the sweet corn. Within the strip in the center were planted short transverse rows of the check (*ga ga su su*) and of the modified hybrids (*Ga ga su su*). Rows were two feet apart and hills were two feet apart in the row. Seedlings were thinned to one per hill.

To insure a full stand, extra cultures



EXPERIMENTAL LAYOUT

Figure 2

The first segment shows the beginning of series I. The second segment includes the end of series I and the beginning of series II. The long rows of field corn (*Su Su ga ga*) were extended beyond the short transverse rows of sweet corn (*su su*) to provide a fairly uniform supply of contaminating starchy pollen (*Su*).

of each stock were started outside the experimental area for replacements. Eighteen dead or apparently dying sweet corn plants were replaced by transplanting from these cultures.

The experiment was laid out in two series. In series I, with one *su su Ga ga* row to four *su su ga ga* rows, approximately one-tenth of all the *su* pollen carried *Ga*. In series II, with four *su su Ga ga* rows to one *su su ga ga* row, about four-tenths of all *su* pollen carried *Ga*. The experiment was divided in this manner to test the possibility of an increase in the effectiveness of *Ga* as the concentration of *Ga* pollen is increased and actual field conditions are approached.

In series I, each of the six *Ga ga* rows (5, 10, 15, 20, 25, and 30) was compared with the two adjacent check rows. In series II, each of the six check rows (40, 45, etc.) was compared with the two adjacent *Ga ga* rows.

When the grains were ripe enough for classification, the first ear of each plant was harvested as a sample. If, as was true of a few plants, the first ear bore fewer than 200 grains, the second ear was added to the sample.

Starchy and sugary grains were counted. The incidence of contamination was computed by dividing the number of starchy grains by the total number of grains.

Results

In this experiment, the incidence of contamination was remarkably low, less than one-third of the incidence found in a small-scale preliminary test two years earlier (see Figure 1). Since the present experiment was laid out in a small bottomland clearing, it is assumed that shelter afforded by surrouunding hills and forest trees hindered the transfer of pollen. Moreover, the long rows of starchy corn were planted on two different dates, ten days apart. From this circumstance, it may be assumed that the actual supply of *ga Su* pollen was

much lower during the critical period than the diagram (Figure 2) would suggest. Possibly, it was lower than in the preliminary test. In any case, the results from the two experiments are in close agreement when expressed as the ratio of contamination in the *Ga ga* hybrids to contamination in the *ga ga* control.

Data from series I are presented in some detail (table I). The mean incidence of contamination for the *Ga ga* hybrids is 0.01232 and the mean incidence for the *ga ga* check is 0.04340. The difference is 0.03109 ± 0.00885. This difference is 3.5 times its standard error with five degrees of freedom and is regarded as significant.

The data from series II are similar but more consistent and with a somewhat greater difference. The mean incidence for the *Ga ga* hybrids is 0.01381 and for the check 0.05911. The difference, 0.04530, is 6.6 times its standard error.

A third test suggested itself during the course of the experiment. In series II, the *Ga ga* rows not adjacent to the *ga ga* check rows were presumably exposed to a lower concentration of available *ga su* pollen than were adjacent rows and thus more closely approximated field conditions under which *Ga ga* hybrids would be grown in a solid stand. These rows (42, 43, 47, etc.) were sampled. The two end rows (38 and 67) were not sampled since their position may have involved a relatively low concentration of *su* pollen. Except for this omission, non-adjacent rows were compared with check rows in the same way as adjacent rows. Again a significant difference, 0.04849±0.00725, in favor of the *Ga ga* hybrids was found.

That *Ga* is effective in reducing contaminations seems to have been amply demonstrated.

The possibility of increase in effectiveness with increase in the proportion of *Ga* pollen remains to be examined. The

TABLE I. EFFECTIVENESS OF Ga IN REDUCING STARCHY CONTAMINATION

(Data from Series I)

Golden Cross Bantam (ga ga control)				Modified Golden Cross Bantam (Ga ga)				
Row	Sugary grains	Starchy grains	Incidence of contamination	Row	Sugary grains	Starchy grains	Incidence of contamination	Difference in incidence
4	1772	169	0.07184	5	2031	30	0.01456	0.05728
6	1936	118						
9	1454	123	0.06763	10	2121	19	0.00888	0.05875
11	1634	101						
14	1818	74	0.03614	15	2002	23	0.01136	0.02478
16	1836	63						
19	1840	73	0.02539	20	1864	14	0.00745	0.01794
21	1999	27						
24	1747	36	0.02311	25	1825	30	0.01617	0.00694
26	1804	48						
29	1920	75	0.03631	30	1908	30	0.01548	0.02083
31	1849	67						
Mean			0.04340				0.01232	0.03109 ±0.00885

three differences obtained may be more fairly compared when expressed as percentage reduction from the incidence of contamination in the check. In the order of increasing proportion of *Ga su* pollen they are:

Series I	71.6% ± 20.4%
Series II	
Rows adjacent to check	76.6% ± 11.8%
Rows not adjacent to check	82.0% ± 12.3%

The agreement with the expectation of increased effectiveness is gratifying but the errors involved are such that little or no significance may be attached to this apparent correlation. The experiment has therefore failed to give conclusive direct evidence that *Ga* becomes more effective as the proportion of *Ga* pollen increases.

Discussion

Notwithstanding the inadequacy of statistical support, there seem to be valid reasons for believing that effectiveness actually does increase as the concentration of *Ga* pollen increases. The presence of this gene has been found to prevent most of the contaminations that normally occur. *Ga* can prevent the contamination of any particular flower only if a *Ga su* pollen grain happens to reach the silk before or soon after a *ga Su* pollen grain reaches it. It is obvious that the more abundant the supply of *Ga su* pollen, the more likely this is to happen. Since frequency is a function of probability, it follows that increasing the concentration of *Ga su* pollen must result in lowering the incidence of contamination.

The limit of improvement by this means is uncertain. The proportion of *Ga su* pollen could be raised to 50 per cent by growing the *Ga ga* hybrids in pure stand and to 100 per cent by using a hybrid homozygous for *Ga*. The figures based on tests by hand pollinations would suggest a possible reduction in contamination between 92 and 100 per cent but there is no reason to assume that the reduction in open-pollinated material would necessarily fall within this range. It might, however, exceed, by a substantial margin, the average of about 77 per cent obtained in this experiment.

Summary

The gene, *Ga*, has been substituted for *ga* in one of the parents of the sweet corn hybrid, Golden Cross Bantam, to produce slightly modified Golden Cross Bantam hybrids of the genotype *Ga ga*.

In such hybrids, *Ga* has been found to eliminate about three-fourths of the naturally occurring contaminations by wind-borne pollen from starchy corn.

Reasons are given for believing that *Ga* can be utilized to bring about a further reduction in starchy contaminations.

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1. Emerson, R. A. *Genetics* 19:137. 1934.
2. Mangelsdorf, P. C., and D. F. Jones. *Genetics* 11: 423. 1926.
3. Perry, H. S. *Elisha Mitchell Scientific Soc. Journ.* 54: 187. 1938. (Abstract *Proc. N. C. Acad. of Science.*)

✦

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GENETICS OF SESAME

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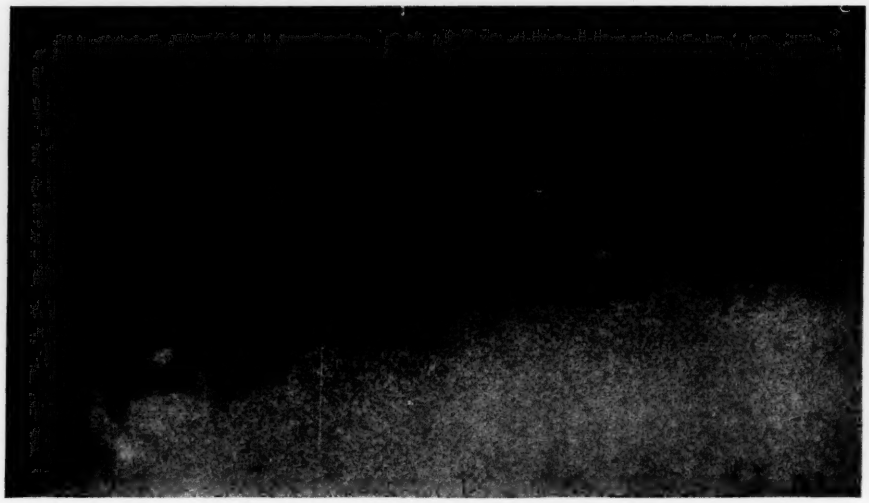


LEAF GLANDS
Figure 3

The glands on the foliage of a sesame plant consist of tetrads of cells supported on a short stalk. It appears that plants well-equipped with glands are more resistant to drought than plants with bare leaf surfaces.

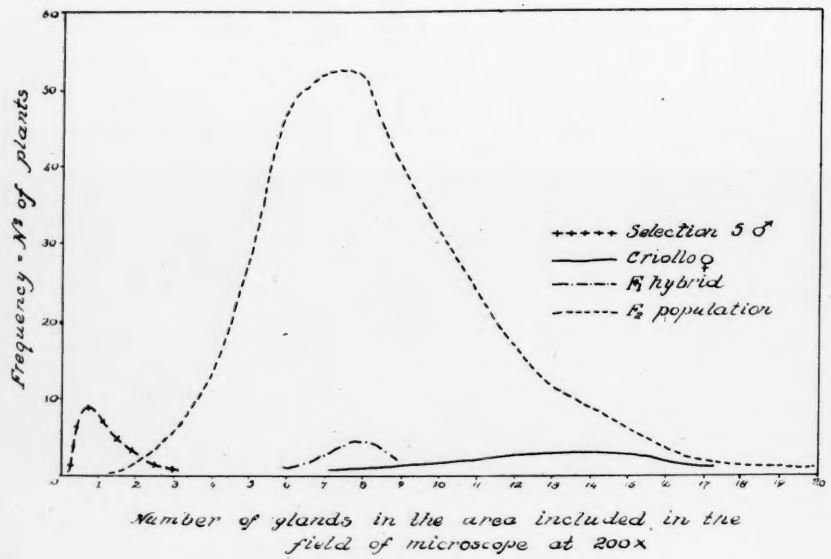
IN connection with experiments to develop varieties of sesame (*Sesamum indicum* L.) adapted to culture in Venezuela, a large number of variant forms has been noted. Some of these have been saved and progenies raised in experiments to determine their mode of transmission. A few have obvious agronomic importance, such as resistance to pests and pathogens. Others are deleterious, and information regarding their inheritance will facilitate their elimination from commercial varieties. The greater number are mainly of interest as comprising an abundant reservoir of genetic material in a fecund and easily grown species. In this contribution, the author will describe four of these characters: number of leaves and capsules per node, and three distinct variations in the nature and distribution of leaf glands and leaf hairs. A later communication will describe and give data on the inheritance of four other characters.

Inheritance of the Number of Foliar Glands*

One of the distinguishing characteristics of sesame is the presence of glandular hairs on the leaves, stems, flowers, and seed pods. Each gland consists of a tetrad of cells supported by a short stalk (Figure 3). The number of these glands per plant varies considerably in different varieties of sesame.

The exact function of these "mucilage"-bearing structures is unknown. According to field observations in 1941,

*With Rafael D. Cortes, Agronomist.


Frequency - Nº of plants
Selection 5 ♂
Criollo ♀
F1 hybrid
F2 population
Number of glands in the area included in the field of microscope at 200×

DISTRIBUTION OF GLAND NUMBER

Figure 4

Distribution in gland number in parent population (Selection 5 and Criollo), the first hybrid generation, and a second hybrid generation of 328 plants. The intermediate distribution of the F_1 hybrids and the lack of any clear dichotomy in the F_2 distribution indicates that gland number is controlled by several genes.

during a period of drought, the varieties with many glands showed less wilting than the types with few glands. On the other hand, during a period of excess rainfall, the varieties of the latter type were more resistant to "wet feet" than were the more glabrous plants. This indicates that the number of glands is probably directly correlated with resistance to drought, and reciprocally correlated with resistance to excess water.

Genetic Studies

For information regarding the mode of inheritance of the number of glands, the variety *Criollo*, a form characterized by millions of glands, and *Selection 5*, with only a few, were crossed and data were collected on the first and second generations.

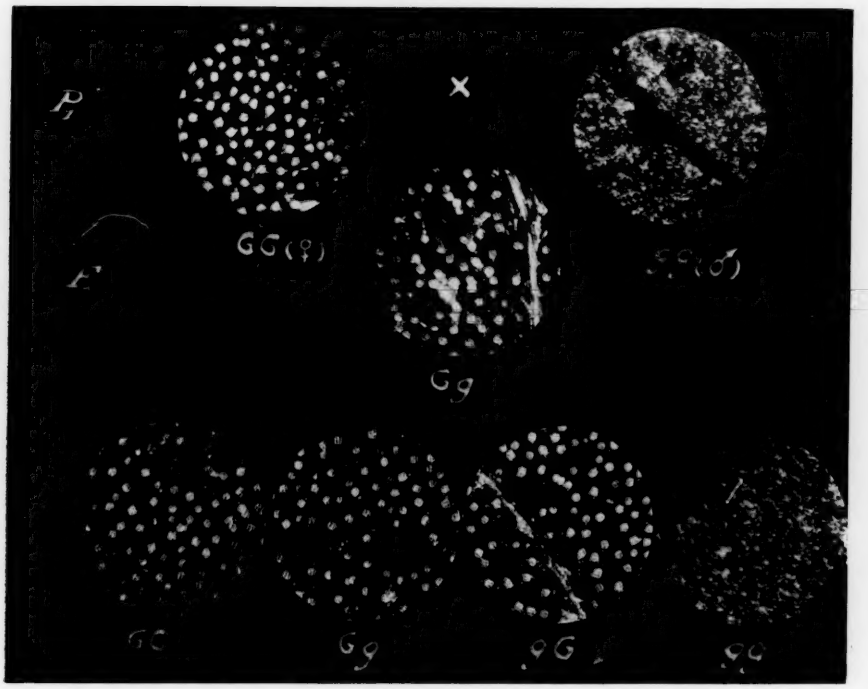
In examining individual plants for the number of glands, it was important to know which leaves could be used as an index for the average number per plant. One leaf was taken from each node of plants three feet high and placed in 70 per cent alcohol. Before examining a leaf with the microscope, it was submerged in water to wash out the alcohol, and then set at an angle to drain off the excess water.

By placing the microscope near a window so that the leaves were illuminated from above, there was no difficulty in counting the glands. A magnification of ×200 gave a field of suitable size.

The microscope was focused in three different regions of the leaf and the number of glands in each area was counted; later an average of the three counts was taken.

Results

When such data were obtained for each leaf it was noted that the small leaves in the upper part of a plant had more glands per area than the large leaves near the base. Leaves from nodes 8 to 12 had the average number of



INHERITANCE OF GLABROUS LEAF SURFACES

Figure 5

Photomicrographs of small areas of leaves from the parental plants, their F_1 hybrid, and four F_2 plants illustrate the simple inheritance of the glabrous condition.

glands per plant. This was true in each of the parental varieties and in the F_1 hybrids. Consequently, any one of these five central leaves can be used as an index for the number of glands per plant. Hence it is not necessary to count the number of glands in all the leaves or to measure the total area. This index system was used to obtain data on the parental varieties, and the F_1 and F_2 generation (Figure 4).

Dominance of the extremely glandular type is incomplete in the first generation and the frequency of the distribution of 328 plants in the second generation gives a somewhat skewed frequency curve, indicating quantitative inheritance.

Glabrous Leaves

A different genetic situation is encountered when plants of the glabrous type are crossed with plants with many glands. Here a simple mendelian inheritance is demonstrated.

In a field of approximately three thousand sesame plants, four glabrous plants were found which differ from the others by the entire absence of glands and pubescence.

Seeds from selfed flowers on each of the four plants gave glabrous seedlings. Those from flowers pollinated artificially with pollen of pubescent plants, gave pubescent seedlings, demonstrating that the character pubescent is dominant over glabrous. The segregation observed in the second generation of these crosses is given in Table I.

TABLE I. Frequency of glabrous and non-glabrous plants in the second generation.

	Observed	Calculated (3:1)	Difference
Non-glabrous	1423	1460	37
Glabrous	524	487	37

These data show that the character glabrous is differentiated by a single gene, designated by the symbol *g*, and its normal allele, by *G* (Figure 5).

The classification of glabrous and non-glabrous plants can be made at any time during the life cycle of the plant. even with the first pair of true leaves. With a little practice it is not necessary to use a lens. Due to the ease of classification, and to the fact that glabrous plants are fully as vigorous as non-glabrous plants, this is an especially useful character in genetic studies. It has already been used in obtaining an estimation of the amount of natural hybridization in sesame.*

Number of Leaves, Capsules, and Rows of Seeds per Node

One of the characters common to sesame varieties from Venezuela, Colombia, Guatemala, Honduras, Mexico, Brazil, India, China and Nicaragua is the disposition of the leaves in pairs with two leaves per node. Although this character is remarkably constant, we have observed since our experiments were begun in 1940, a few plants with three leaves per node, instead of two. Since the seed pods are borne in the axils of the leaves, there is a high correlation between the number of leaves and the number of capsules per node.

A typical sesame plant with paired leaves is shown in Figure 8. In plants of this type there are four possible combinations with respect to the number of rows of seed and the number of capsules per node. These four types illustrated in the Figure are common among the different varieties of sesame.

The rare type with three leaves at each node is shown in Figure 9. In this case there are also four possible combinations with respect to the number of rows of seed and of capsules per node.

Since 1940, five generations of these abnormal plants have been studied to determine their economic value and the inheritance of the character. It has not been possible to obtain varieties of this type because the variant forms have not been found to breed true. The progeny of a plant like (*E*) gives plants like (*A*); (*F*) gives plants like (*B*); (*G*) gives plants like (*C*), and (*H*) like (*D*) (Figures 8 and 9).

Plants with three leaves per node are more frequent in varieties like (*B*) and (*D*), having eight rows of seed per pod. But uniformity through selective inbreeding has not been achieved.

Absence of Glands on the Dorsal Surface of Leaves

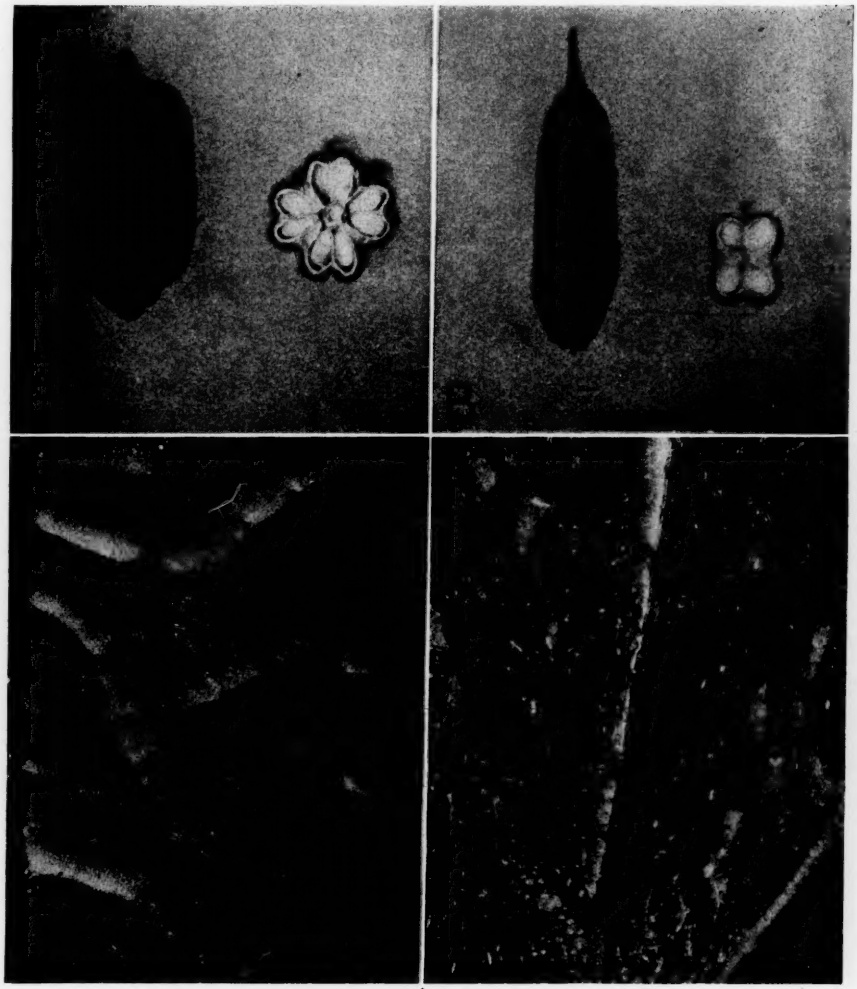
Another varietal difference was noted wherein two varieties (*Jaffa* from Venezuela and *White* from India) differed from all others in the absence of glands on the dorsal surface of the leaves. This difference was so striking that these two varieties were easily distinguished from those with glands on the dorsal surface of the leaves, even without the use of a lens.

Several months later as the plants approached maturity, these two varieties were found to differ from the others in still another character (Figure 6). Their fruits were tetracarpellate with eight rows of seeds instead of the normal paired carpel with four rows per pod.

Crosses were made between *Jaffa* and *White*, and between these two varieties and others, including *Criollo, Colombia,* and *Guatemala.* The first generation hybrid, *Jaffa* × *White,* was without glands on the dorsal surface of the leaves and had tetracarpellate fruits, demonstrating that the same gene for this character is found in these two varieties.

The first generation hybrids *Jaffa* × *Criollo, Jaffa* × *Colombia, Jaffa* × *Guatemala, White* × *Criollo, White* × *Colombia, White* × *Guatemala,* and the reciprocals of these crosses, had glands on the dorsal surface of the leaves and bicarpellate fruits, indicating that the presence of glands is dominant over their absence and that bicarpellate fruits are

*Langham, D. G. *Jour. Hered.* 35:254-256. 1944.



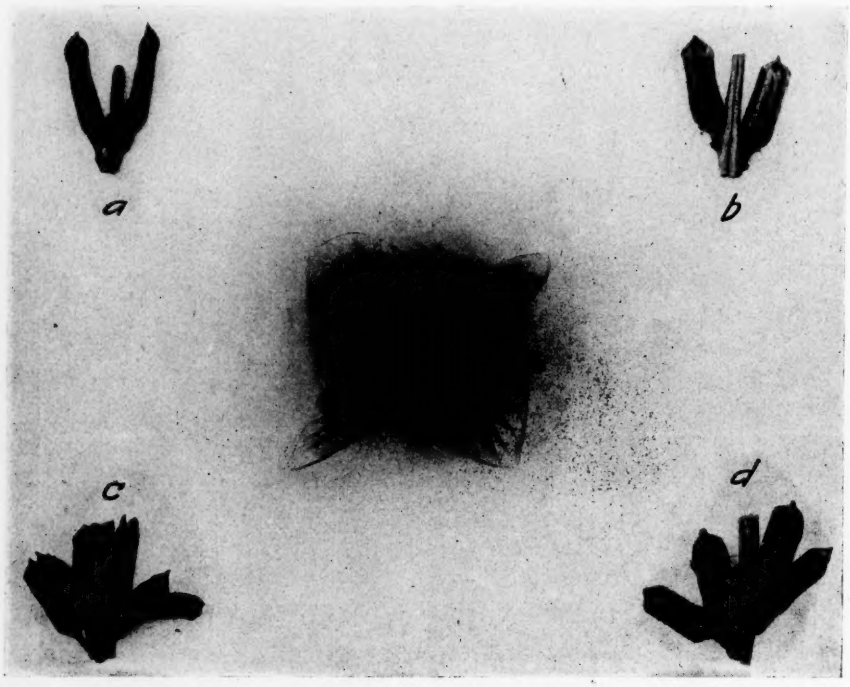
ABSENCE OF GLANDS ON DORSAL LEAF SURFACE

Figure 6

Part of a leaf surface from a plant without glands on the dorsal surface, and the associated tetracarpellate seed-pods are shown at A. A leaf with glandular dorsal surface and bicarpellate seed-pods are shown at B. The correlation between leaf surface and seed-pods has been complete in the material studied, indicating that a single gene, rather than close linkage between two genes, conditions these two characters.

dominant over tetracarpellate.

In the second generation there were plants with *no* glands on the dorsal surface, plants with *many* glands, and others with all gradations between the two extremes. The intergrades were disregarded in this study, but approximately two hundred plants of the types without glands and with glands on the dorsal surface were staked in the seedling stage.



TWO-LEAVED NODES

Figure 7

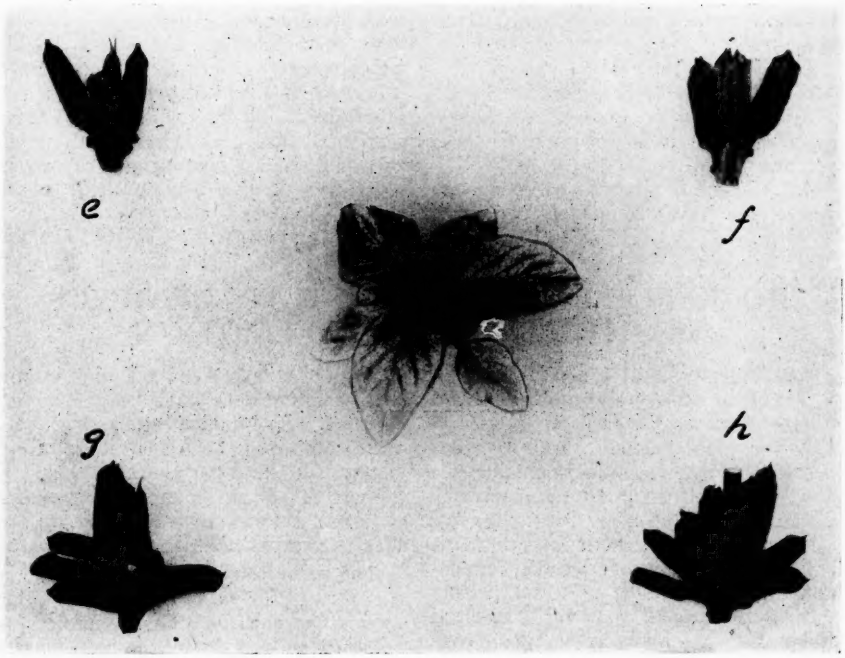
The number of leaves per node is a very constant character in sesame, though a few plants having more are found (Figure 8). The number of seed-capsules per axil and of rows per capsule varies, as is shown in the illustration:

	Axils per node	Capsules per axil	Rows per capsule	Capsules per node	Rows per node
a	2	1	4	2	8
b	2	1	8	2	16
c	2	3	4	6	24
d	2	3	8	6	48

Six weeks later perfect correlations were found between absence of glands and tetracarpellate fruits (*ss*) and between presence of glands and bicarpellate fruits (*SS* or *Ss*) in these segregating populations. This correlation was true only for the presence or absence of glands on the dorsal surface of the leaves; the number of glands on the ventral surface of the leaves was wholly independent of the type of fruit.

For convenience in taking notes in genetic studies and in breeding work, the symbol *s* has been adopted to indicate the gene conditioning absence of glands from the dorsal surface of the leaves, and the symbol *S* for the dominant allele conditioning the presence of glands on the dorsal surface.

Further evidence on the relation between *s* and tetracarpellate fruits and *S* and bicarpellate fruits has been obtained by making crosses between plants *within* the variety *Jaffa*. The original collection of this variety is a mixture of about 88 per cent of plants with tetracarpellate fruits and clean-topped leaves (*ss*) and 12 per cent of plants with bicarpellate



THREE-LEAVED NODE

Figure 8

The three-leaved plants show an increase in the number of capsules and of rows per node. The data on the axils shown here are given below. In crosses between two-leaved and three-leaved plants the hybrids are usually two-leaved, but an occasional hybrid plant with three leaves is found. It has not been possible to fix the three-leaved type by inbreeding.

	Axils per node	per axil	Rows per capsule	per node	Rows per node
e	3	1	4	3	12
f	3	1	8	3	BD
g	3	3	4	9	36
h	3	3	8	9	72

fruits and glandular upper leaf surface (*SS* or *Ss*). When these two types of plants are crossed, the first generation hybrid has tetracarpellate fruits and the leaves are *without* glands on the dorsal surface. This dominance of tetracarpellate over bicarpellate seed pods is a direct contrast to the results of the crosses listed above. It appears from this result that the dominant allele in the *Jaffa* variety is different from that in the glandular-leaf varieties *Criollo, Colombia* and *Guatemala*. This situation has not been investigated further. The most significant fact is that tetracarpellate fruits and absence of dorsal surface leaf-glands are always associated, regardless of whether they are dominant or recessive in the particular cross in question. This association between type of fruit and presence or absence of glands on the dorsal surface of the seedling leaves has been a useful tool in the practical plant breeding work with sesame in this Department. Further studies are in progress.

Summary

Four genetic types are described in sesame, with notes on their mode of in-

heritance as indicated by F_1 and F_2 progeny tests:

1. Glabrous leaves;
2. Number of foliar glands;
3. Variation in number of leaves, capsules and number of rows of seeds per node; and
4. Absence of glands on dorsal surface of the leaves completely correlated with tetracarpellate fruits.

Of these four characters and character-complexes 1 and 2 are complexly inherited, 3 shows a simple mendelian inheritance, and in 4 absence of dorsal glands is always associated with tetracarpelate fruits. This pleiotropic pair is sometimes dominant and sometimes recessive in crosses.

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ROCKEFELLER GRANT TO STUDY GENETICS OF INTELLIGENCE AND EMOTION

ON May 7 the Rockefeller Foundation announced a grant of $282,000 to the Roscoe B. Jackson Memorial Laboratory for studies over a five-year period of genetic factors in intelligence and emotional variation in mammals. This most interesting project may mark a turning-point in genetic research as it applies to questions of peculiar importance in human society.

The Roscoe B. Jackson Memorial Laboratory has made a very great contribution to cancer research by making available highly inbred and hereditarily uniform strains of mice offering a great variety of constitutional differences in cancer incidence and in resistance to carcenogenic substances. The mouse is ideal for such studies because it shows remarkable parallelism with human cancer.

In a somewhat similar way the dog offers unique advantages for experiments in inheritance of mental and emotional qualities. Of prime importance, breeds of dogs already exist which differ greatly in size, endocrine constitution, intelligence, emotional qualities, etc. These breeds are highly uniform in size and conformation and often in color, but are less alike in mental and emotional qualities. Even in respect to these the inter-breed differences are very small compared with the differences between some of the breeds. Hence, dog breeders have already gone far in the standardization of strains uniform in respect to the characters it is proposed to investigate. In no other mammal is there a range of standardized variation in any way comparable to that already existing in dogs. And furthermore, Dr. Little points out that in such qualities as affection, loyalty, and persistence, the dog is perhaps closer to man than monkeys or apes, a form almost as unsatisfactory as genetic material as man himself.

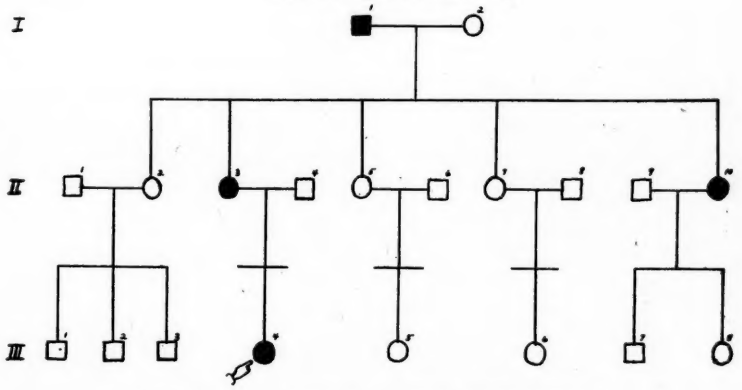
The project will be able to build on the work of several other workers. The most comprehensive of these earlier investigations was that of the late Charles Stockard, whose studies of the influences of the endocrine glands in determining constitution and psyche in dogs give an excellent groundwork. The work of breeding Seeing Eye dogs at Morristown, New Jersey and elsewhere, under the direction of Mr. Elliott Humphrey, leaves no doubt that certain mental and emotional qualities are definitely inherited.

At the Beltsville Research Station a project that promised important developments along these lines was initiated some years ago (see *Yearbook of U. S. Dept. Agr. 1937*. P. 1327). A modest beginning was made by crossing certain very different breeds of dogs and observing the behavior of the hybrids. Unfortunately the project was discontinued after three years, before any results could reasonably be expected. It is encouraging that the research just announced is set up to allow enough time so that the possibilities may be adequately explored. Hardly more than that is to be expected

(*Continued on page* 147)

ABSENCE OF OLFACTORY SENSATION

ROSEMARY CALLAN MAINLAND
Glenn Ellyn, Illinois



PEDIGREE OF TOTAL "SMELL BLINDNESS"
Figure 9

Transmission for three generations of a total inability to smell. Taste discrimination was slightly affected. A dominant inheritance of this deficiency is suggested.

A PEDIGREE of the absence of olfactory sensation in a Russian family has been reported by Glaser.[3] The factor was handed down from an affected father to his daughter and to her two sons. Glaser thought that the factor was probably sex-linked. Blakeslee[1] has reported a case in which certain individuals were able to smell pink verbenas and not red verbenas while other individuals were able to detect an odor in the red verbenas and not in the pink. Two persons tested were able to detect odors in both the red and pink verbenas. Parr[4] states that there are different sensory thresholds in different individuals for the same given stimulus, and in some instances a person's threshold may be so high that he may be considered "blind" to the stimulus. Blakeslee and Fox[2] tested several persons for various substances such as quinine, P.T.C., salt, Hydrochloric acid, etc. They found that there were great variations in the thresholds of the same individual for different substances, and that an acute perception for one substance was not correlated with other perceptions.

This pedigree traces the absence of olfactory sensation through three generations (Figure 9). The defect is apparently caused by a single autosomal dominant gene since it is passed through three generations from an affected parent to part of the offspring. Normal parents give normal offspring. In the case of the marriage of an affected person, II-10, to a normal person, II-9, both offspring are apparently normal, but the offspring are too young for testing.

The olfactory and gustatory tests were run on the propositus using a normal person as a control (See Table I). In the olfactory tests the propositus was unable to distinguish any odor from oil of cloves, butyl mercaptan, lysol, oil of peppermint, methyl salicylate, oil of cedarwood, amyl propionate, and oil of anise. She got a burning sensation in her nostrils from the fumes of oil of cajeput, amyl acetate and ammonium hydroxide. The control was able to distinguish the various odors accurately. All substances used for testing were in

identical opaque bottles so that they could not have been distinguished by color, etc.

For the gustatory test both individuals were blindfolded. The propositus was able to taste most of the substances such as oil of wintergreen, oil of peppermint, hydrochloric acid, sodium bicarbonate, quinine sulfate, and powdered sugar. She was unable to distinguish between sweet and sweet chocolate. She also said that cloves was cinnamon. The control was able to distinguish between all the substances by tasting them. Both the propositus and the control said that P.T.C. tasted like paper.

Summary

A pedigree in which there is an absence of olfactory sensation is presented. The trait in this pedigree appears to be dependent on a single dominant autosomal gene.

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2. Blakeslee, A. F., and A. L. Fox. *Jour. of Hered.* 23:97-110. 1932.
3. Glaser, Otto. *Science*, N.S. 48:647-648. 1918.
4. Parr, Leland W. *Jour. of Hered.* 25: 187-190. 1934.

TABLE I. Olfactory and Gustatory reactions of totally "smell-blind" person and a normal control.

OLFACTORY TEST

Substance Tested	Affected Person	Control
Oil of Cloves	Nothing	Cloves
Oil of Cajeput	Nothing—burns nostrils slightly	Definite odor
Butyl mercaptan	Nothing	Skunk
Lysol	Nothing	Lysol
Oil of Peppermint	Nothing	Peppermint
Methyl salicylate (Oil of Wintergreen)	Nothing	Wintergreen
Amyl acetate (Banana Oil)	Nothing—burns nostrils slightly	Banana
Oil of Cedarwood	Nothing	Cedar
Ammonium hydroxide	Nothing—burns nostrils	Ammonia
Amyl propionate (Oil of Spearmint)	Nothing	Spearmint
Oil of Anise (Oil of Licorice)	Nothing	Licorice

GUSTATORY TEST

Powdered sugar + Oil of Wintergreen	Mint	Mint
Powdered sugar + Oil of Peppermint	Peppermint	Peppermint
Hydrochloric acid	Salty—sour	Salty—sour
Quinine sulfate	Bitter	Bitter
Powdered sugar	Sweet	Sweet
Powdered sugar + Chocolate	Sweet	Sweet chocolate
Powdered sugar + Cloves	Cinnamon	Cloves
P.T.C. Paper	Paper	Paper
Soda	Sour—bitter—finally said soda	Soda

COMPLETE ALBINISM IN THE MUD PUPPY, NECTURUS

F. B. HUTT
Cornell University, Ithaca, New York

RED AND WHITE
Figure 10

Only a color photograph could do justice to this rare creature, for the blood-filled gills form a red ruff almost completely surrounding its neck.

THE albinotic mud puppy, *Necturus maculosus,* shown in Figure 10 was sent by Dr. D. L. Gamble of Ward's Natural Science Establishment, Rochester, New York, to Professor A. H. Wright of this institution. He, in turn, kindly made it available to the writer for purposes of this note. The specimen was received in November, 1943, was maintained alive for about two weeks and was then preserved and placed in the collection of the Department of Zoölogy.

The illustration of it, though showing a striking contrast with the greyish brown coloration that is normal in this species, cannot do full justice to this specimen. It showed no sign of the "ghost pigmentation" that causes faint patterns in animals with imperfect albinism. As in all complete albinos, its eyes lacked melanin and appeared reddish from the blood circulating through the retina and iris. However, the contrast between the pinkish white skin and red eyes that makes complete albinism a striking phenomenon in any species was accentuated in this case by the external gills. Since these are large in *Necturus* and highly vascularized, they appeared to form almost a red ruff around the white neck of the albino. When it was kept for several hours in a refrigerator, with resultant reduction of activity and circulation to a low level, the gills became pale pink in color, but, when the animal was placed in a small laboratory aquarium at room temperature, the gills became a bright blood red. As may be seen in Figure 10, the right hind foot

had only three toes instead of four.

The albino had been received by Ward's along with normal mud puppies from Menasha, Wisconsin. Correspondence with Mr. Joe Pawlack, who collected it, revealed that it came from Lac Butte des Morts, which is connected with Lake Winnebago in east central Wisconsin. According to Bishop's[2] distribution, it would therefore belong to the sub-species, *Necturus maculosus stictus* Bishop. The albino was a male and fully adult, being 275 mm. long. Bishop[2] gives the range in length for this sub-species as 238 to 362 mm. and the average length as 292 mm.

So far as the writer can determine, the only adult albinotic specimen previously reported in this species is one taken from Oneida Lake, New York, and described by Corrington.[5] It was a female and apparently a complete albino except for chocolate tips on the toes. If any such markings were present in the specimen shown in Figure 10, they were not noticed by the writer, or by several other observers who handled it before it went into formalin, and could not be detected in later examinations. Professor S. C. Bishop has advised the writer that he also has an adult albinotic mud puppy in his collection at the University of Rochester. It was received through Ward's Establishment, as was the present specimen, and came originally from Oshkosh, Wisconsin. Considering the rarity of albinos in this species, it is of interest to note that Oshkosh is on Lake Winnebago, and that Professor Bishop's specimen and this later one apparently were caught at points within about 30 miles of each other.

Cahn and Shumway[4] referred to "two albino larvae" of this species, but did not state whether these were complete albinos with red eyes or black-eyed whites. They were preserved when only 18 mm. long.

In birds and mammals, complete albinos are unusually sensitive to strong light and consequently develop photophobia. Their vision is impaired and they are usually more conspicuous than their normally colored mates. For all these reasons the mutation undoubtedly lowers somewhat the chances of survival in wild birds and mammals. The comparative rarity of adult albinos suggests that under natural conditions few of them live to reproduce and that the sporadic specimens occasionally reported are the offspring of normally-pigmented heterozygous parents rather than of homozygous albinos.

In *Necturus,* however, complete albinism may be somewhat less of a handicap. The very small eyes of mud puppies, together with the fact that they normally inhabit lake bottoms and feed at night, suggest that good vision is less important to them than to most animals. Cave-dwelling urodeles of the genera *Proteus, Typhlotriton* and *Typhlomolge* are all blind when adult. From this standpoint, it would seem that a mutation to albinism has more chance of being preserved and multiplied in a population of mud puppies than in birds and mammals. On the other hand, the whiteness and the red gills of the albino may make it more conspicuous and hence more subject to the attacks of predators. These last are undoubtedly more abundant in the lakes where *Necturus* abounds than in the caves inhabited by the urodeles mentioned above, all of which are white as well as blind.

Rarity of Albinos

At any rate, albinism is apparently no more common in *Necturus* than in other animals. Mr. Pawlack writes that in ten years of fishing for mud puppies he has seen only three albinos among some 25,000 caught, and that this one was the "most perfect specimen." This probably means that only one was a complete albino. Dr. W. C. Senning of the New York State Conservation Department, who, while teaching zoology at Cornell University, collected many mud puppies from Cayuga Lake, writes as follows:

My records show that from 1925 to 1935, inclusive, I collected 16,147 Necturi from Cayuga Lake. From 1935 to 1940, when I left Cornell, I collected several thousand additional specimens, but I did not keep accurate records covering the period. While several specimens among the number were somewhat lighter

in color than usual, I saw only one that lacked most of its pigment. This was more than likely only a partial albino. I do not recall that it had pink eyes.

Apart from Corrington's albino in *Necturus,* the only other published record of complete albinism in the Caudata (Urodela) known to the writer is that of Banta and Gortner[1] who kept for some time an albinotic salamander of the species now known as *Eurycea bislineata.* In this case, as in some of the albinos reported in the Salientia (Anura), the mutation eliminated the melanic pigments but not the yellow ones.

Records of albinism in other Amphibia were reviewed by Boulenger.[3] While albinotic larvae have been noted in several species, the only adults known to him were in *Rana temporaria* and *Alytes obstetricans.* In the latter species, Héron-Royer[7] succeeded in getting a few larvae from two albinotic parents and found them to be all albinos. The only other genetic study of albinism in amphibians is apparently that of Haecker,[6] which showed that partial albinism in the axolotl, *Ambystoma tigrinum,* is a simple recessive mutation. Albinos have been known in captive axolotls for many years. It is not clear whether these include any complete albinos, or whether all have the partial type studied by Haecker in which the larvae are white with red eyes but develop dark pigment on the head and back as they grow older.

Summary

A completely albinotic, adult, male mud puppy, presumably belonging to the sub-species, *Necturus maculosus stictus* Bishop, was taken from Lac Butte des Morts, near Lake Winnebago in Wisconsin. Some data are cited which indicate that albinism is no more common in this species than in other animals.

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Rockefeller Grant

(*Continued from page* 142)

in five years. We may be confident that the leads opened up will be so promising that ways will be found to continue the research beyond that time.

In announcing the grant Dr. C. C. Little, Director of the Jackson Laboratory, made the following statement regarding plans and objectives:

The age-old controvery on the relative importance of heredity and environment still has value although not in the mutually exclusive way that popular opinion would lead one to believe. It has become evident that neither heredity nor environment could go far without the other.

If, for example, the tiny, concentrated centers of chemical organization known as genes —the basic unit of heredity—had no living organism provided by food and growth on which and in which to express their directive powers they would be incapable of description, measurement or identification. If, on the other hand, living material grew and multiplied without the directive hand of heredity there would be no permanency of the various forms of life and the course of evolution would not be possible.

Human life as it can be measured and recorded consists of a partnership between the two forces of heredity and of environment. There is plenty of room in our definition to include non-material or spiritual forces.

One does not need to deny their existence or to belittle their importance. By their very nature, however, they are not subject to material laws and cannot, therefore, be measured, reproduced, recorded or organized by educators or scientists.

They must always act on a foundation of physical and physiological material if they

are to be identified with a particular individual and the study of the variations in these physical and physiological factors remains a fascinating and highly important scientific problem for educators and biologists.

There are many handicaps in attempting to pursue controlled scientific studies in these fields when human material is used. The normal human being is a highly complex and volatile combination of heredity and environment. His various emotional patterns and intellectual capacities are interwoven and are influenced to various degrees by habit, association, memory and all of the factors that go to make up his continuing experience both consciously and subconsciously.

It is desirable, therefore, to consider how far we can make use of animal material to help us understand the various elements which enter into the physical and physiological composition of human individuals of different emotional and intellectual capacities.

Animal material is available in may types. Some of these are relatively primitive and limited while others are much more highly organized and resemble man closely.

Naturally among the higher forms the anthropoid apes have been the favorite material. It is, however, true that their physiological and psychological organization is for the most part as difficult to analyze as is that of humans.

It seems probable that such a type as the dog may well present a type in which most of the basic elements of intellectual or emotional patterns are not only present but have actually by selective breeding been accentuated and segregated to a degree that makes them easier to recognize and analyze.

It is, for example, well known that emotional type may be importantly influenced by activity of the endocrine glands. It is also known that form varies with the over or under secretion of endocrines. The various breeds of domestic dogs have been developed in many directions both of form, temperament and function.

The studies of Stockard and his associates have provided a foundation of morphological, physiological and psychological data on certain experiments with dogs.

It is now the plan to set up a series of studies based on the attempt to analyze the roles of genetics and of environment in determining both breed and individual differences in dogs.

This work will have the advantage of close association with genetic work on the smaller laboratory animals such as mice, rats, hamsters, guinea pigs and rabbits.

When problems of social dominance and adjustment are under consideration it may also be possible to use some of the gregarious types like sheep and goats.

When techniques like transfer of ova, experimental endocrine unbalance, foster nursing and hybridization of breeds are utilized, interesting results should be obtained.

Fortunately the present work is being planned to cover a long enough period so that no pressure to produce hasty or incomplete results need be felt.

At Bar Harbor the work will be located at the Hamilton Station—a tract of fifty-six acres of farm land with a number of large barns and buildings already available. It is also planned to utilize help from a number of farms where individual dogs can be kept for breeding purposes.

A number of the standard breeds of dogs will be studied. Among these will undoubtedly be included Dachshunds, English Springer Spaniels, Dalmatians, Chows, Brussels Griffons, Boston Terriers, Beagles, Poodles and several others.

Species-Antigens in Ducks

By means of immunological techniques, the red blood cells from Mallards, Muscovies and hybrids between these species have been examined for antigenic similarities and differences. Each species possessed antigens specific to itself as well as others which were shared. The cells of the F_1's examined contained the major part of the antigens specific to each of the parental species and presumably all those common to both. In addition, the hybrids possessed a new or "hybrid" substance which was not found in the cells of either parent. The existence of the hybrid character was demonstrated by two independent methods. It was not possible by the tests employed to fractionate this substance.

Differences in antigens specific to Muscovy were noted among the hybrids from each of two matings. These results would be expected on a genetic basis, by virtue of the segregation of genes controlling those characters which were carried in the heterozygous state by the respective Muscovy parents. For example in one family comprising 25 hybrids from a Muscovy male, the offspring possessed one or the other of two antigens. These contrasting antigens presumably were controlled by one or more genes on a single pair of chromosomes of Muscovy—W. H. McGibbon. *Genetics* 29:418. 1944.

INHERITANCE IN LADY BEETLES

III—Crosses between variants of *Hippodamia quinquesignata* and between this species and *H. convergens**

A. Franklin Shull

THE experiments here described started with a small collection (23 beetles) from the mountains near Logan, Utah, obtained through the courtesy of Professor G. F. Knowlton and Dr. Stephen L. Wood. They were all in one hibernating mass, belonged to the species *Hippodamia quinquesignata* Kby. (determined by Professor Wm. C. Stehr), and exhibited certain striking differences in pattern. As soon as virgin females of the most distinct variants could be obtained, they were crossed with one another and with the spotless form of *H. convergens* from California. After two or three generations wild spotless *H. convergens* was again introduced, and some of the descendants of this cross were mated with the spotted form of *H. convergens*.

Phenotypes of *H. quinquesignata*

The elytral patterns of the original collection from Logan can be described in terms of the numerical scheme adopted by the author[2] for *H. convergens* with its six spots zigzagging from the anterior outer (humeral) spot (no. 1) back to the apical spot (no. 6). In the majority of individuals the first two spots were connected by a band extending across both elytra near the front margin. Sometimes this band was broad with smooth edges (Figure 11*A*), sometimes narrow (*B*) or irregular, or even completely interrupted (*C*). In a smaller number this band was lacking, leaving only the two spots on each elytron corresponding to spots 1 and 2 of *H. convergens*, spot 2 being regularly joined to the scutellar stripe (Figure 12*A*).

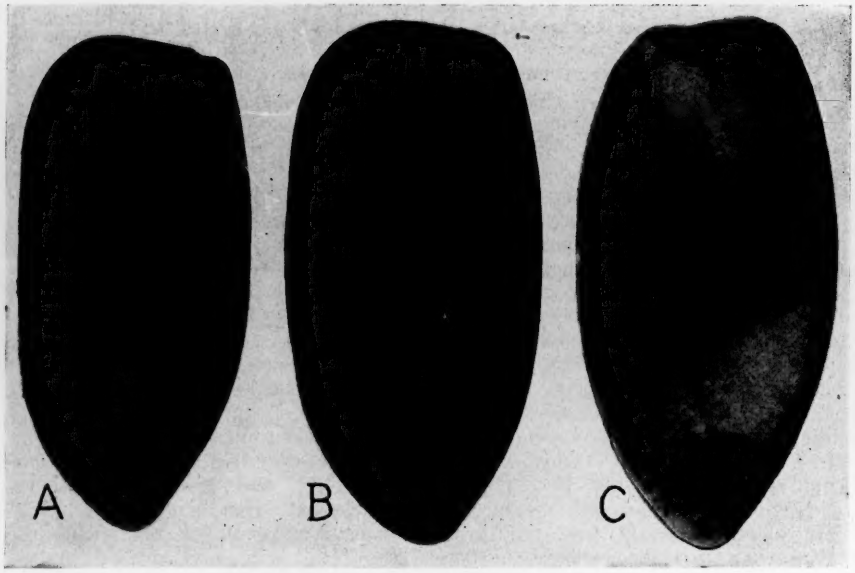
In nearly half of the Logan beetles there was a spot behind this band, near the lateral border of the elytron (Figure 11*A, B*), corresponding to spot 3 of *H. convergens*.

Just back of the middle of each elytron, in most of the beetles, was an oblique band (Figure 11*A-C*), usually having a jog or slight constriction near its middle which showed it to be a fusion of spots in the 4 and 5 positions of *H. convergens*. In three beetles of the original collections spots 4 and 5 were completely separate, with 1 and 2 still connected in a band; and in later generations deep constriction of this band (Figure 12*B*) and complete separation of the spots (*C*) were accompanied by the separation also of spots 1 and 2.

It is possible that a fourth variable character could have been studied, for nearly a third of the Logan collection lacked spot no. 6, a condition almost realized in Figure 11*B*. However, in the limited numbers of pairs of parents which could be reared along with experiments already in progress when the collection was received, emphasis was placed on other contrasts. None of the parents chosen lacked the 6-spot, and it was rarely absent in later generations. This fact itself suggests strongly that presence or absence of this spot has a genetic basis, but offers little ground for judging the mode of its inheritance.

Another collection of beetles of this same species should be mentioned merely for a census of its phenotypes, though they did not contribute to any of the experiments. These beetles were collected in the active season, along with other species, at Caldwell, Idaho, by Dr. Harriet Smith. They showed the same general variations as did the Logan group, though spots 1 and 2 were a little

*Contribution from the Department of Zoology, University of Michigan. Aided by a grant from the Faculty Research Fund of the University of Michigan and a gift from Mrs. S. Ralph Lazrus.



IRREGULARITIES OF PATTERNS

Figure 11

Variations of the pattern of *Hippodamia quinquesignata*, especially the anterior band, but also absence of lateral spot (*C*) and near absence of apical (*B*). The left elytron is shown in all figures.

more often separate (absence of the anterior band), spot 3 was a little less often absent, and spot 6 was a little more often absent. Spots 4 and 5 (of the postmedian band) were separate in almost exactly the same proportion of individuals as at Logan.

These two collections, though both small, coming from two adjoining states, indicate by their similarity that they probably represent rather well the wild population of that general region.

Numerical Rating of Patterns

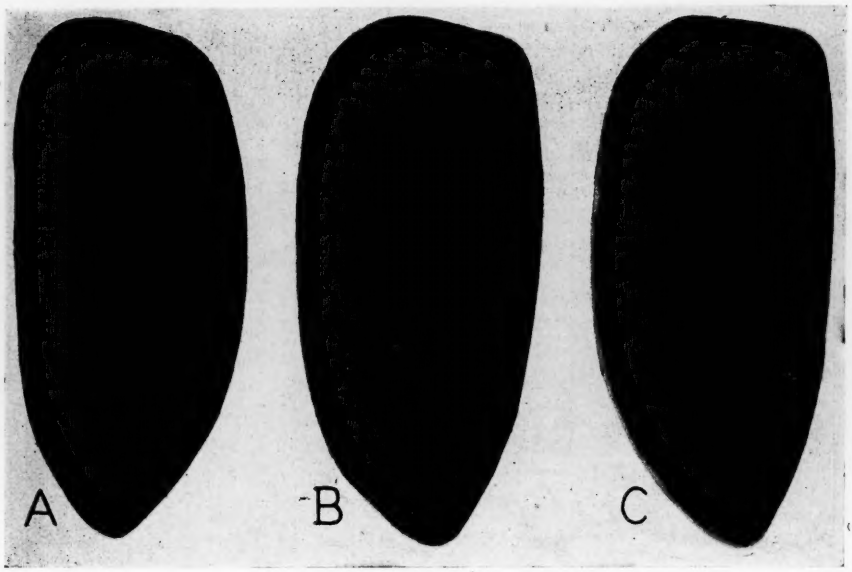
All the results of the 63 different experiments are presented in Table I. The amount of detail there given is the result of a compromise between limitations of space and the need of a basis of judgment. To save many illustrations, the patterns are represented by numerical signs now to be described.

In the fourth and fifth columns of the table are given the phenotypic formulas of the two parents. The six digits in these formulas refer to the six spots, according to the scheme devised[2] for *H. convergens*. Absence of a given spot is indicated by a zero in its position among the six spots. Size of the spots is indicated by the size of the number, up to a maximum which was originally 4 but now is 7.

A band connecting spots 1 and 2 is indicated by underscoring the digits in the first two positions. The size of the band is indicated by the size of the numbers thus underlined. The first two digits separated by a hyphen indicate that the band was narrow and quite irregular or even interrupted. The two numbers separated by an apostrophe mean that there was no anterior band at all.

Spot no. 3 follows, between two virgules; absence is indicated by zero, size by the digits 1 to 4.

The digits in fourth and fifth position



BANDS BECOME SPOTS

Figure 12

Separation of anterior band into two distinct spots, resembling *H. lecontei;* also separation of postmedian band into two spots, as in *H. convergens.*

represent the postmedian band. If underlined, these spots were distinctly joined; if separated by a hyphen, the merger was slight or doubtful; if separated by an apostrophe, the spots were distinct, though they were mostly rather close together until about Experiment 319, when the *H. convergens* influence (of no postmedian band) was becoming dominant.

The presence and size of the apical spot are indicated by the digit in sixth position, following the third virgule.

When a parent was not available for rating, and records were inadequate to indicate sizes of spots, the six positions are represented by the letters *a-f*. Spotless beetles could not be represented by the above scheme, but merely by six digits indicating the size of the spots which were present. A question mark after a phenotypic formula means that the beetle has been lost and the ratings of the spots are taken from records.

Course of the Experiments

From the original Utah collection four matings were made, two pairs possessing anterior bands (spots 1 and 2 joined), two pairs with these spots separate. The females in these four matings may not have been virgin; indeed, in one of them she certainly was not.

The course of the experiments after these first four matings is indicated in the second and third columns of Table I by the numbers of experiments from whose offspring the parents were selected. The abbreviated words in these columns indicate that parents were taken from wild collections obtained in Yosemite Valley, California, and in Colorado, respectively. The genealogy is not an ideal one; it is the series of experiments which succeeded. To the difficulty created by declining vigor resulting perhaps from inbreeding, to which attention was called in an earlier paper,[2] must be added a peculiarity of this particular

TABLE I. Data from all the experiments; see text for description.

Exp. No.	Source of Parents		Phenotypes of Parents		Assumed Genotypes of Parents		Possible Genotypes of Offspring	Phenotypes of Offspring.										
	♀	♂	♀	♂	♀	♂		S	s	1-2	1-2	1'2	3^0	3^1	3^2	3^3	3^4	3^5	4-5	4-5	4'5
258	Wild	Wild	3 5/0/5'5/3	6 7/0/5 5/3?	ss qq tt ff	ss qq tt ff	ss qq tt ff	0	52	48	4	0	48	0	2	2	0	0	50	0	2
	Utah	Utah	6 7/0/5 5/3				ss Qq Tt Ff														
259	Wild	Wild	2 5/0/5 5/4	4-4/0/4 4/1	ss qq tt ff	ss Qq tt ff	ss qq tt ff	0	42	25	14	3	34	6	2	0	0	0	42	0	0
	Utah	Utah				Tt	ss Qq Tt														
260	Wild	Wild	0'4/3/4 4/3	3'4/3/4'4/3	ss QQ TT ff	ss Qq Tt Ff	ss QQ Tt Ff	0	47	0	0	47	0	0	5	18	24	0	43	2	2
	Utah	Utah				ff	ss Qq Tt ff														
262	Wild	Wild	a'b/c/4 e/f	a'b/c/4 e/f	ss QQ TT ff	ss QQ Tt Ff	ss QQ Tt Ff	0	12	0	0	12	0	0	0	7	5	0	12	0	0
	Utah	Utah					ss Qq Tt ff														
277	258	258	5 6/0/5 5/3	6 6/0/5 5/4	ss qq tt ff	ss qq tt ff	ss qq tt ff	0	1	1	0	0	1	0	0	0	0	0	1	0	0
278	258	258	5 6/3/5 5/3	4 6/0/5 5/4	ss qq Tt ff	ss qq tt ff	ss qq Tt ff	0	17	17	0	0	13	0	2	1	1	0	17	0	0
							ss qq tt ff														
279	260	264	2'4/4/4 4/4	001000	ss Qq Tt ff	88 QQ TT Ff	Ss QQ TT Ff	14	0	0	0	0	0	0	0	0	0	0	0	0	0
							ss Qq Tt ff														
280	259	260	4 6/0/5 5/4?	4'4/4/4 4/4?	ss qq tt ff	ss QQ TT ff	ss QQ Tt Ff	0	4	0	0	4	0	0	0	3	1	0	4	0	0
281	259	260	4 5/0/5 5/4	4'5/3/4 4/2	ss qq tt ff	ss Qq Tt ff	ss QQ Tt ff	0	8	3	0	5	1	1	2	0	4	0	8	0	0
							ss Qq Tt ff														
283	258	258	4 6/4/5 5/3?	4 5/4/4 4/3?	ss qq Tt ff	ss QQ Tt ff	ss QQ Tt Ff	0	1	1	0	0	0	0	0	0	1	0	1	0	0
285	259	260	5 4/0/4 4/2?	2'4/3/4 5/3	ss qq tt ff	ss Qq Tt ff	ss QQ Tt Ff	0	6	3	1	2	0	1	1	3	1	0	6	0	0
							ss Qq Tt ff														
286	258	258	5 6/0/5 5/4	4 6/0/5 5/4	ss qq tt ff	ss qq tt ff	ss qq tt ff	0	3	3	0	0	3	0	0	0	0	0	2	1	0
287	259	260	4 5/0/5 5/4	1'4/2/3'4/3	ss qq tt ff	ss Qq Tt Ff	ss QQ Tt Ff	0	7	4	0	3	0	3	2	2	0	0	4	2	1
							ss Qq Tt ff														
288	260	260	2'4/3/4 5/4	4'4/3/4 5/3	ss Qq TT Ff	ss QQ TT ff	ss QQ Tt Ff	0	10	0	0	10	0	1	4	4	1	0	6	2	2
							ss Qq Tt ff														
289	259	260	2 6/2/5 5/4	2'4/4/5 5/3	ss qq Tt ff	ss Qq Tt ff	ss Qq Tt Ff	0	8	4	0	4	1	0	2	3	2	0	7	0	1
							ss Qq tt ff														
290	259	260	1 6/0/4 4/3	3'5/4/4 5/4	ss qq tt ff	ss Qq Tt Ff	ss Qq Tt Ff	0	21	5	16	0	10	1	7	2	1	0	11	3	7
							ss Qq tt ff														
291	279	279	021000	010000	Ss Qq TT Ff	Ss Qq Tt Ff	88 QQ TT Ff	33	5	0	0	5	0	1	3	1	0	0	2	0	3
							Ss QQ Tt Ff														
293	279	279	053000	012000	Ss Qq TT Ff	Ss Qq TT Ff	88 QQ TT Ff	16	0	0	0	0	0	0	0	0	0	0	0	0	0
							Ss QQ Tt Ff														
294	279	288	054000	3'4/2/4 5/4	Ss Qq TT Ff	ss QQ TT ff	Ss QQ TT Ff	18	16	0	0	16	0	1	6	6	3	0	6	0	10
							ss Qq Tt ff														
295	281	279	a'b/c/4 e/f	011010	ss Qq Tt ff	Ss QQ TT ff	Ss QQ TT ff	8	9	0	0	9	0	1	4	0	4	0	9	0	0
							ss Qq Tt ff														
297	288	288	2'5/3/3'5/3	2'5/4/4'4/2	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	2	0	0	2	0	0	2	1	0	0	0	0	2
298	288	288	3'4/2/4 5/4	2'4/3/5 5/4	ss QQ TT ff	ss QQ Tt ff	ss QQ Tt ff	0	4	0	0	4	0	1	2	1	0	0	4	0	0
299	281	278	4'5/4/5 4/2	4 6/0/4 5/4	ss Qq Tt ff	ss qq tt ff	ss Qq Tt ff	0	18	11	7	0	10	1	1	4	2	0	17	0	1
							ss Qq tt ff														
300	281	286	4 6/1/5 5/3	4 5/0/5-5/3	ss qq tt ff	ss qq tt ff	ss Qq Tt ff	0	5	5	0	0	5	0	0	0	0	0	5	0	0
302	289	289	5'5/4/5 5/3	4'4/3/5 5/3	ss Qq Tt ff	ss Qq Tt ff	ss Qq Tt Ff	0	1	0	0	1	0	0	1	0	0	0	1	0	0
							ss Qq tt ff														
305	290	279	2-4/2/4'5/3?	122000?	ss Qq Tt Ff	Ss QQ Tt Ff	Ss QQ TT Ff	3	3	0	0	3	1	1	0	0	1	0	2	0	1
							ss Qq Tt Ff														
							ss Qq tt ff														
307	295	Wild Yos.	5'5/4/5 5/3	002000?	ss QQ Tt ff	Ss QQ TT Ff	Ss QQ TT Ff	6	5	0	0	5	0	0	3	0	2	0	0	0	5
							ss Qq Tt ff														
309	295	293	0422317	142000?	Ss QQ TT Ff	88 QQ TT Ff	88 QQ TT Ff	1	0	0	0	0	0	0	0	0	0	0	0	0	0
311	299	294	4 6/3/5 5/3	052000	ss qq Tt ff	Ss QQ Tt ff	Ss QQ Tt Ff	6	6	5	0	1	0	2	1	3	0	0	6	0	0
							ss qq Tt ff														
312	299	291	4 6/4/5 5/3	001000	ss qq Tt ff	Ss Qq Tt Ff	Ss Qq Tt Ff	5	4	3	0	1	1	1	0	0	1	0	2	0	2
							ss qq Tt ff														
313	295	293	044000	141000?	Ss Qq TT ff	Ss Qq TT ff	88 Qq TT ff	14	6	0	0	6	0	0	0	1	5	0	6	0	0
							Ss Qq Tt ff														
							ss qq tt ff														
314	305	293	000000	052000	Ss Qq Tt Ff	Ss Qq TT Ff	88 Qq TT Ff	10	3	1	0	2	0	0	0	0	3	0	0	1	2
							Ss Qq Tt Ff														
							ss qq tt ff														
315	305	294	4'4/4/4 5/4	000000	ss Qq TT ff	Ss Qq TT Ff	Ss Qq TT Ff	1	4	0	0	4	0	0	1	0	3	0	1	1	2
							ss Qq tt ff														
316	302	293	4'4/3/5 5/3	012000	ss Qq Tt ff	Ss qq TT ff	Ss Qq TT ff	4	2	0	0	2	0	0	0	1	1	0	2	0	0
							ss Qq Tt ff														
319	307	Wild Yos.	032000	5'5/4/6'6/7?	Ss Qq Tt Ff	ss QQ TT Ff	Ss QQ TT Ff	14	31	0	0	31	0	2	3	5	20	1	1	0	30
							ss Qq Tt Ff														
320	307	Wild Yos.	000000	5'4/4/4'5/5	Ss QQ Tt Ff	ss QQ TT Ff	Ss QQ TT Ff	12	9	0	0	9	0	1	1	2	5	0	1	1	7
							ss Qq Tt Ff														
322	319	Wild Yos.	6'6/4/6'5/4	4'4/3/5'5/4	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	20	0	0	20	0	0	2	14	4	0	5	0	15
							ss qq TT Ff														
323	319	Wild Yos.	6'5/4/6'4/4	4'4/3/4'4/5	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	40	0	0	40	0	0	0	8	32	0	3	3	34
							ss QQ Tt Ff														
324	320	Wild Yos.	001000	4'4/3/4'4/5	Ss QQ TT Ff	ss QQ TT Ff	Ss QQ TT Ff	17	21	0	0	21	0	0	0	8	13	0	4	0	17
							ss QQ Tt Ff														
325	319	Wild Yos.	043000	4'5/4/4'5/5	Ss QQ TT Ff	ss QQ TT Ff	Ss QQ TT Ff	11	12	0	0	12	0	0	0	1	10	1	1	0	11
							ss QQ Tt Ff														
326	320	Wild Yos.	5'5/4/6-6/4	3'5/3/4'4/4	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	33	0	0	33	0	0	7	14	12	0	4	3	26
							ss Qq TT Ff														
							ss Qq Tt ff														
327	320	Wild Col.	6'5/4/5-5/4	4'4/4/4'5/4	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	25	0	0	25	0	0	2	10	13	0	2	0	23
		Yos.					ss Qq Tt Ff														
333	327	Wild Col.	3'3/4/4'5/4	0'3/0/3'0/0	ss QQ TT Ff	ss QQ Tt Ff	ss QQ Tt Ff	0	10	0	0	10	0	1	4	4	1	0	0	0	10
334	327	Wild Col.	5'4/4/5'5/5	3'3/3/0'2/3	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	16	0	0	16	0	0	2	13	1	0	0	0	16
335	327	Wild Col.	4'4/4/4'5/4	3'0/0/3'2/0	ss QQ TT Ff	ss QQ Tt Ff	ss QQ Tt Ff	0	30	0	0	30	0	2	8	15	5	0	1	0	29
							ss Qq TT Ff														
336	327	Wild Col.	4'4/4/4'5/4	0'3/4/0'2/2	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	20	0	0	20	0	0	0	1	19	0	0	0	20
337	326	Wild Col.	2'4/2/4'4/4	0'3/0/2'3/1	ss QQ TT Ff	ss QQ Tt Ff	ss QQ Tt Ff	0	16	0	0	16	0	5	4	6	1	0	0	0	16
338	326	Wild Col.	5'4/4/5 5/4	4'4/3/4'4/2	ss QQ TT ff	ss QQ TT Ff	ss QQ TT Ff	0	19	0	0	19	0	0	1	9	9	0	1	0	18
339	326	Wild Col.	5'4/4/5 5/4	4'5/4/5'4/4	ss QQ TT ff	ss QQ TT Ff	ss QQ TT Ff	0	10	0	0	10	0	0	0	1	9	0	6	1	3
							ss QQ Tt ff														
340	338	329	5'4/4/5'4/4	3'4/3/4'4/3	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	9	0	0	9	0	0	1	4	4	0	0	0	9
							ss QQ Tt Ff														
341	337	329	3'4/4/4'5/4?	4'4/4/4'5/4	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	3	0	0	3	0	0	0	3	0	0	0	0	3
							ss QQ Tt Ff														
342	337	330	4'4/4/4'5/4	4'4/4/4'4/4	ss QQ Tt FF	ss QQ TT Ff	ss QQ TT Ff	0	10	0	0	10	0	0	2	2	6	0	0	0	10
							ss QQ Tt Ff														
344	337	329	0'3/2/4'5/4	2'4/3/4'4/4	ss QQ Tt FF	ss QQ TT Ff	ss QQ TT Ff	0	2	0	0	2	0	0	1	1	0	0	0	0	2
							ss QQ Tt ff														
345	339	329	5'4/4/5 5/3	3'4/3/4'4/4	ss QQ TT ff	ss QQ TT Ff	ss QQ TT Ff	0	1	0	0	1	0	0	0	0	1	0	0	0	1
347	337	330	0'5/1/4'5/4	4'4/4/4'5/4	ss QQ Tt FF	ss QQ Tt Ff	ss QQ TT Ff	0	10	0	0	10	2	1	3	3	1	0	0	0	10
							ss Qq Tt ff														
							ss Qq tt ff														
348	336	329	1'5/4/4'4/5	2'4/4/4'4/4	ss QQ TT FF	ss QQ TT Ff	ss QQ TT Ff	0	6	0	0	6	0	0	0	1	5	0	0	0	6
351	338	329	5'4/4/4'4/4	4'4/3/4'4/3	ss QQ TT Ff	ss QQ TT Ff	ss QQ TT Ff	0	11	0	0	11	0	1	2	7	1	0	0	0	11
							ss QQ Tt Ff														
352	339	331	3'2/1/4'3/2	3'4/3/4'4/4	ss QQ Tt Ff	ss QQ Tt Ff	ss QQ TT Ff	0	8	0	0	8	3	1	1	0	3	0	0	0	8
							ss QQ Tt Ff														
							ss QQ tt ff														
353	335	329	1'2/2/4'4/1	1'4/4/4'4/4	ss QQ Tt FF	ss QQ Tt FF	ss QQ TT Ff	0	1	0	0	1	0	0	0	1	0	0	0	0	1
							ss QQ Tt ff														
358	348	352	0'4/4/4'5/5	1'2/0/2'2/3	ss QQ TT FF	ss QQ Tt Ff	ss QQ Tt Ff	0	66	0	0	66	1	3	21	21	20	0	1	0	65
							ss Qq Tt Ff														
362	358	358	1'4/4/4'5/5	3'4/4/4'5/4	ss QQ Tt FF	ss QQ Tt Ff	ss QQ TT Ff	0	2	0	0	2	0	0	1	1	0	0	0	0	2
							ss Qq Tt Ff														
364	358	358	3'4/3/4'5/5	3'4/4/5'5/5	ss QQ Tt FF	ss QQ Tt Ff	ss QQ TT Ff	0	4	0	0	4	0	0	2	1	1	0	0	0	4
							ss Qq Tt Ff														
366	358	358	0'5/3/3'4/3	1'4/4/3'4/3	ss QQ Tt FF	ss QQ Tt FF	ss QQ TT Ff	0	6	0	0	6	0	2	1	2	1	0	0	0	6
							ss Qq Tt Ff														

investigation, namely, the absence of one sex from many of the progenies. This feature made it impossible to obtain an F_2 or other inbred generation in a number of crucial situations.

Certain experiment numbers in the columns of parents do not appear in the first column as a part of the main line of descent. Experiment 264 was a mating of two spotless beetles of the species *H. convergens* from Placerville, California. Experiments 329, 330 and 331 were matings of wild *H. convergens* from Colorado. These experiments were designed to provide a stock of spotless and spotted members of that species.

Phenotypes of Offspring

In classifying the progeny of the various crosses, in the last fourteen columns of the table, space is saved by assuming that no two of the characters are linked. There is no obvious indication of linkage, since the various recombinations of characters are found. Owing to the obstacles described in the preceding section, matings to test linkage would have been difficult. Though certain combinations are more frequent in the progenies as a group, this excess is readily traceable to the combinations that happened to be present in the parents used. To list all the combinations separately would require a table many times as large, with probably less resulting clarity concerning the main genetic features. Each of the four phenotypic characters is therefore classified independently.

In the first two of the last 14 columns (phenotypes) are indicated the numbers of progeny which were spotless (*S*) and spotted (*s*). It should be remembered that "spotless" beetles may have spots.[2] The beetles appearing in the spotted columns are then classified further with respect to each of the other features of their pattern. The next three columns are devoted to the anterior band; the meaning of the headings of these columns has already been explained in the section on "Numerical Rating of Patterns." The next six columns relate to the presence and size of spot no. 3; the symbol 3^0 means that this spot was missing, while the symbols 3^1 to 3^5 indicate that spot 3 was present and of sizes 1 to 5. The last three columns classify the offspring with respect to the postmedian band (spots 4 and 5), under headings which were explained earlier.

The Genetic Explanation

Because of the difficulty of making certain desirable crosses, and because of the decline in vigor over a series of generations, it has not been possible to determine the heredity of each character in the usual fashion by the use of homozygous material. Nevertheless, a scheme has been devised which furnishes a rather satisfactory explanation of the bulk of the data. The great majority of the results can be explained by assuming four main pairs of genes, along with supplementary genes which modify the dominance or otherwise affect the expression of some of these four. One of the principal pairs of genes relates to the spotless or spotted pattern, on which earlier results have been published for one of the species.[2] A second pair concerns the anterior band connecting spots 1 and 2; a third determines the presence or absence of spot 3; and a fourth relates to the merger of spots 4 and 5 into the postmedian band.

Spotless *versus* Spotted

The results concerning the spotless pattern as contrasted with the spotted are rather clear. The spotless pattern (gene *S*) is dominant over the spotted (*s*). The nearest approach to a contradiction of this conclusion is found in Experiment 293 in which the parents must, from their source, be regarded as heterozygous (*Ss*), yet all their 16 offspring are spotless. The one-fourth recessive class could be absent by accident; also a mutation to spotless could have made one of the parents a homozygote; or a recessive lethal might have accompanied the spotted pattern in this instance. The other results with spotless and spotted are quite regular. In forty matings of spotted with spotted, only spotted progeny were produced (this

character is recessive). In twelve matings of spotted with spotless the progeny are 105 spotless and 122 spotted (a 1:1 ratio). In four crosses of spotless by spotless the offspring are 73 spotless and 14 spotted (a 3:1 ratio).

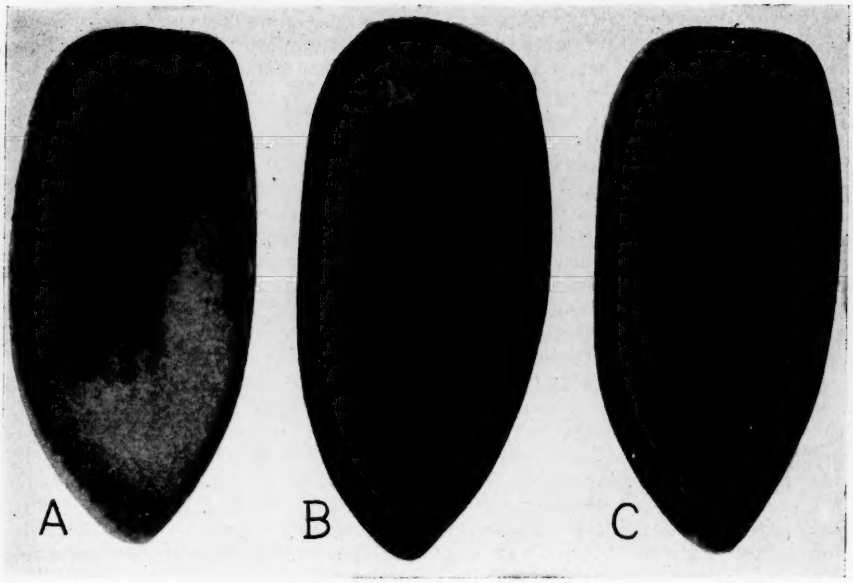
Certain other results indicate that a nearly spotless condition may be attained without gene *S*. From earlier work with Michigan and California beetles[2] it had been concluded that a "spotless" beetle (a possessor of gene *S*) might have posterior spots about three-fourths as great as the maximum spots of the spotted pattern. It was possible to fix that point as the statistical boundary between the two patterns, though it was recognized as probable that spotted beetles might have smaller spots, and spotless ones have larger spots, than this dividing point indicated. The present work shows that some beetles from Colorado far transcend this limit in one direction. The fathers in Experiment 333 to 337 were all considered spotless when used in matings; but since none of their offspring was necessarily regarded as spotless, and only about three of them could have been regarded as spotless on the Michigan-California basis, they are considered spotted and their phenotypes and genotypes are formulated in accord with that conclusion. In another instance one of the offspring of Experiment 366, largely descended from the Colorado strain, was given a phenotypic rating of 033010, and would have been classified as spotless were it not that both of its parents were spotted. This one beetle could be the result of a mutation; otherwise it indicates that a nearly spotless pattern may result in the absence of gene *S*. It was not possible to breed this beetle further to settle this point.

An additional point of interest is that the spotless gene suppresses the spots of *H. quinquesignata* to about the same extent as those of *H. convergens*. Most "spotless" individuals had some spots, particularly the anterior ones. For the most part these spots were rounded and reduced, without any indication of their specific form. In several specimens, however, spot no. 2 had diffuse extensions which were interpreted as the characteristic contributions of that spot to the anterior band. In Figure 13*A* the second spot is spread lightly toward both spot no. 1 and the scutellar stripe; in *B* it expands only toward the scutellar stripe; and in *C* the whole spot is diffuse but of a shape indicating an approach to the stripe. These beetles are from Experiments 311, 314 and 312, respectively, in which the anterior band might be either present or absent. One mating was made in an attempt to prove whether these extensions did actually represent the anterior band, but no offspring were obtained.

The Anterior Band

Though the band connecting spots 1 and 2 is very variable in expression, a large part of its determination may be attributed to one pair of genes. In general, it is concluded that the gene for this band (designated *q* from *quinquesignata*) is recessive to separate spots (*Q*). As explained before, the experiments could not always be performed in such a way as to decide which gene is dominant. Many of the crosses between unlike parents produced divided progenies, indicating that one parent was heterozygous, but not showing which parent this was. Nevertheless, among the many pertinent tests were the following. In five experiments in which both parents had the anterior band, all the offspring (27 of them) had the band; at least one of the parents must have been homozygous. In four experiments between a banded and a bandless beetle, 15 offspring had the band, 14 lacked it; one parent must have been heterozygous. In one cross between a banded and a bandless, the four offspring were all bandless. While this last result would be possible on the assumption that the band is dominant, it is improbable. Since the above results are compatible with dominance of bandlessness, it is concluded that in general the band connecting spots 1 and 2 is recessive.

Some assumptions have to be made to fit certain results not included in the above clear-cut statement. Dominance



BAND CONCEALED UNDER SPOTLESSNESS

Figure 13

Diffuse 2-spot, interpreted as trace of anterior band underlying the not-quite-dominant spotless gene.

of *Q* (separate spots) is not always complete; it seems necessary to regard the mother of 305 as heterozygous, though she has an irregular or broken band. The father of 259, also necessarily considered a heterozygote, likewise had an interrupted band; but since in this cross the mother may not have been virgin, the father is not surely known. The offspring of Experiment 290 are in like manner better explained on the basis of a nondominant *Q*, since none of them has strictly separate 1- and 2-spots, though half of them would be expected to do so on the alternative assumptions.

The occasional or frequent lack of dominance in this pair of genes may be caused by other genes, so that dominance would be of different grades in different progenies.

Spot Number Three

That presence of the lateral spot behind the anterior band is due to a gene (*T*) dominant over absence of the spot (gene *t*) is concluded from the following evidence. Three early matings between beetles with and without the 3-spot (Exps. 280, 285, 287) yielded only offspring having this spot. Two other matings from the same source, between beetles with and without the 3-spot (Exps. 281, 290), and two similar matings from other sources (Exps. 278, 299) yielded divided progenies, some having 3, others lacking it. None of the matings of this kind yielded only offspring lacking the third spot.

Furthermore, one mating between beetles having the 3-spot produced, among the eight offspring, one which lacked it (Exp. 289). The ratio here is not too great a modification of 3:1, and certainly it does not fit the opposite assumption. It seems necessary to regard presence of spot no. 3 as dominant over its absence.

Some irregularities in the behavior of the *Tt* alleles must be assumed. Thus,

the mother in Experiment 300 is considered to have the genotype *tt* despite her small third spot, to account for a progeny exclusively without spot 3. If gene *t* be thought of as a suppressor of this spot, even the homozygote—so the assumption goes—has not quite suppressed it in this instance.

The father in Experiment 358 raises a question affecting either the choice of his genotype or the adequacy of gene *T* to produce the spot. If this father is *tt*, all the offspring are *Tt* (one nevertheless lacking spot 3), and the next three experiments should yield both types of offspring in the ratio of 3:1 (the one-fourth class being, however, missing). If, to avoid the expectation of beetles lacking the third spot in the progenies of these last three experiments, the father of Experiment 358 be assigned the genotype *Tt*, then gene *T* is not dominant in him. The former alternative has been doubtfully adopted for the table.

Lack of dominance of *T* is hinted at in assigning the genotype *Tt* to the mother in Experiment 347, with her small 3-spot, as if a single *t* could nearly suppress that spot. The divided progeny calls for heterozygosis in both parents. A still greater failure of dominance of *T* is found in the one offspring of Experiment 358 which had no 3-spot. It can not very well be held to be *tt*, for the mother came very largely from recent wild sources and most probably was *TT*. If despite this argument, the mother be regarded as a heterozygote, then half (not just one) of the 66 offspring should lack spot no. 3. The ability of a single *t* occasionally to suppress this spot seems to be distinctly the more likely of the alternative assumptions.

The Postmedian Band

The union or separation of spots 4 and 5 is subject to enough irregularity to call for probably a number of genes. These genes cannot, however, be equal in their effects. There is abundant reason to assume that one of them is far the most important—a principal gene, to which the others are related as modifiers or accessories.

There is some reason to regard the one main gene effecting a fusion of spots 4 and 5 as recessive (gene *f*). In Experiment 307, on this basis, the cross is $ff \times FF$ (the spotless father being regarded, because of the wild population from which he came, as almost necessarily homozygous for genes which would separate spots 4 and 5). The progeny would then be alike, with separate spots, as they are observed to be. If fusion of spots 4 and 5 were dominant, the cross in Experiment 307 would be at best $Ff \times ff$ (with progeny of two kinds) and at worst $FF \times ff$ (with progeny all having the postmedian band). Neither of these requirements is met.

Most other experiments could be brought into conformity by postulating that fusion of spots 4 and 5 is controlled by a dominant gene. On the basis of the evidence outlined in the preceding paragraph, the postmedian band is regarded as recessive (*ff*), while separation is dominant (*FF* or *Ff*). Whichever assumption is made as to dominance, many irregularities are found which require presumably the action of other genes. Some of these difficulties will be pointed out.

After making the best possible set of assumptions for the experiments as a whole, it seems necessary to conclude that the genotype *ff* does not always entail the firm fusion of spots 4 and 5. One of the offspring of Experiment 286 has the two spots barely touching on one side, a little more closely joined on the other; and in one of the offspring of Experiment 289 spots 4 and 5 are completely separate. Nor is *F* always dominant. To account for two kinds of offspring in Experiment 288 it seems necessary to assign the genotype *Ff* to one of the parents, yet both of them have spots 4 and 5 broadly fused. There are other places in the experiments where partial dominance of *F*, or lack of dominance, needs to be assumed.

In Experiments 319-325 and 327, a small number of the offspring have the postmedian band, which could be explained by regarding their fathers as

heterozygous (*Ff*); but were that done, these postmedian bands should be much more numerous. Moreover, these fathers were wild beetles of the species *H. convergens* from California; and if so many individuals chosen at random should be heterozygous, then postmedian bands should appear in natural populations. Spots 4 and 5 are occasionally closer together, and rarely touch, in these populations, but gene *f* if present at all must be rare. The fathers in Experiments 326 and 339 (the latter wild *H. convergens* from Colorado) have been assigned the genotype *Ff*, partly to indicate the general possibility that exists for this whole group of experiments, and partly (in Exp. 339) because of the relatively large number of individuals having joined 4- and 5-spots. Even in this latter experiment, however, the spots were not broadly joined, as in the wild *H. quinquesignata* from which they partly descended; the postmedian band was deeply constricted at its middle.

This latter point—that union of spots 4 and 5 in the hybrids often scarcely produces a band—may suggest one of the explanations of the greater irregularity of this fusion as compared with the spotless condition, the anterior band, and spot No. 3. It is possible that other genes besides *f*—probably a number of them—cause an approach of spots 4 and 5 to one another. *Hippodamia convergens* might possess enough of these to account for the occasional nearness or slight fusion of these spots, but not possess gene *f* at all. The species *H. quinquesignata* could also possess these genes, perhaps as abundantly as does *H. convergens*. If these genes were accessory to genes *F* and *f*, in the sense that they added to or subtracted from the phenotypic effects of these genes, much variation of the band would be accounted for. Another effect of these genes might be modification of the dominance of *F*, but it is hardly necessary to devise any further complications to account for the observed irregularities.

Genotypes of Parents and Offspring

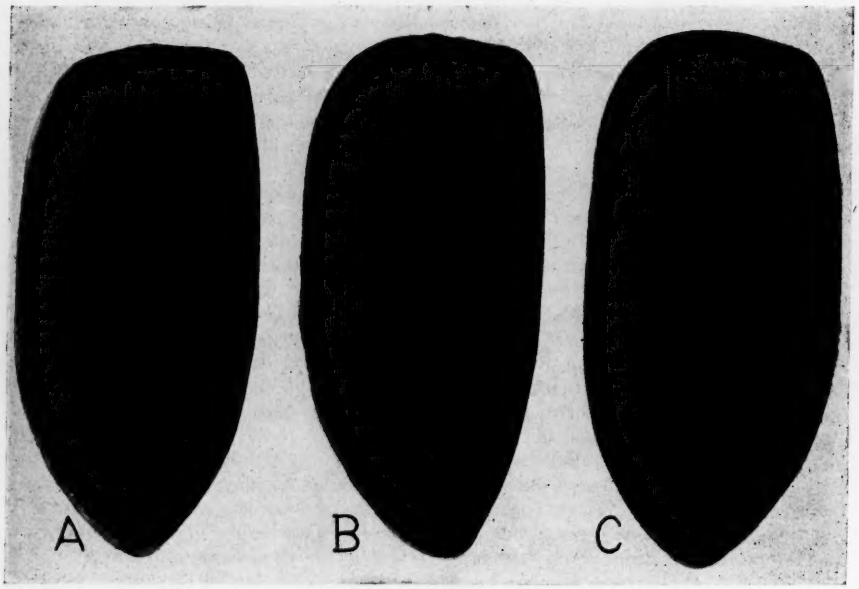
In accord with the foregoing discussion of the four separate characters, possible genotypes have been assigned to parents and offspring in the sixth, seventh and eighth columns of the table. In Experiment 258, two females are given because this was originally intended as a stock. In the first four experiments, the females were not assuredly virgin, hence two genotypes are given to the male in some instances. When the female was known to be virgin, as in all the other experiments, only one genotype is assigned to the male. For the progeny, two or three genotypes are often given. To save space, not all the possible genotypes are given; but those which are required by the phenotypes of the offspring or by subsequent matings are all included. In omitting unnecessary genotypes no particular attention was given to keeping those which would be numerically most probable; it was regarded as satisfactory to indicate a genotype which (1) was possible and (2) would explain the results.

It should be specifically pointed out that the wild Yosemite males introduced in Experiments 307 and 319-327, and the wild Colorado males in Experiments 333-339 were of the species *H. convergens*. Their genotypes were chosen in accord with their phenotypes and with the wild populations from which they were taken.

Attention should also be called to the genotypes *Ff* and *ff* assigned to the males in Experiment 260. The latter of these would represent previous matings of the non-virgin female. The progeny indicate that the earlier matings were much more effective than those which occurred after the isolation of the pair.

The Species Cross

Anyone who examined only the elytral pattern might conclude that the beetle represent in Figure 12*A* is *Hippodamia lecontei* Muls., particularly if the intergrading anterior bands of Figure 11 were unknown, if the hibernation of the two forms together were ignored, and if the 2-spot were firmly joined to the scutellar stripe as in this specimen, to form (on the two elytra together) a three-



APPROACH TO HIPPODAMIA CONVERGENS

Figure 14

Early generation species hybrids resembling one of the ancestral species, *H. convergens.*

pointed star. However, the male genitalia are identical in the beetles with and without the band connecting spots 1 and 2. The genitalia of *lecontei,* which I have not seen, are said to be much shorter than in these forms.

The only species cross in this study is thus between *H. quinquesignata* and *H. convergens,* in Experiment 279. Descendants of this cross were bred together and backcrossed to both species, especially to *H. convergens,* in complex fashion. The details of these crosses may be ascertained from the table. The results indicate, as there shown, that the genetic differences between the species, so far as elytral pattern is concerned, are not very great.

It remains to point out the same conclusion arrived at in another way. How soon, in the generations following the species cross, do individuals appear which are reasonably near either contributing species? Because of the variation within *H. quinquesignata* (presence or absence of the anterior band, for example) it would be difficult to say when that species had been recovered. It would be arbitrary to insist on a wide anterior band when such a band is not always present in nature. It is proposed, therefore, to look only for returns to the pattern of *H. convergens.*

It is unfortunate that the only species cross which succeeded was one in which the *convergens* parent was spotless, since the number of descendants in which the typical pattern could be recognized is thereby greatly reduced. It is also unfortunate that the only successful species cross was made with a *Hippodamia quinquesignata* which already lacked the anterior band. This beetle was also fathered by one in which spots 4 and 5 were separate, but it itself had them broadly connected in a postmedian band; so that, unless gene *F* here lacks dominance, the genotype of the beetle is *ff* and the separation of spots 4 and 5 in its father has been eliminated.

The mother in Experiment 279 still has spot 2 connected broadly with the scutellar stripe, to produce the 3-pointed star which has often been regarded almost as diagnostic of *H. lecontei* but which here is *quinquesignata* as distinguished from *convergens*. Probably, therefore, the only step toward *convergens* which could be regarded as having already been taken in advance of the species cross was the separation of spots 1 and 2.

Close approximation of the *convergens* pattern is reached already in the F_2 generation (Exp. 291). In Figure 14*A* is shown one of the five spotted members of that family. If collected along with *H. convergens*, this beetle would no doubt be regarded as belonging to that species. Two other spotted ones in the same progeny had spots 4 and 5 separate and about as far apart as the one illustrated. All three of these had spot 2 separate from the scutellar stripe.

Other *convergens*-like hybrids are found among the offspring of Experiment 307. To obtain them a spotless F_1 from the species cross was backcrossed to a *lecontei*-like *quinquesignata*, and one of their *lecontei*-like offspring was backcrossed to a spotless wild *convergens*. All five of their spotted offspring, of which Figure 4*B* is one, could have been regarded as *convergens*.

Finally, an F_2 backcross (Exp. 312) produced Figure 14*C*. A spotless F_2 from the species cross was backcrossed to a typical *quinquesignata* with anterior band (whose mother, however, had the *lecontei* pattern). One of their four spotted offspring is shown.

No superior merit is claimed for the arguments advanced in this section, which go to show that the pattern differences between the species are not very complex, as compared with the genetic analysis of the separate characters in the preceding sections which shows the same thing. They should be of some interest, however, to those who are concerned with specific distinctions in nature. It is recognized, of course, that pattern is not the only feature by which the species are judged. The male genitalia, on which taxonomists place considerable reliance, are not here considered.

The Evolution Problem

The purpose of these studies is to throw light on the probable evolution of the Coccinellidae by revealing the genetic relations of species, or of varieties which might be on their way to becoming species. Varieties which show differences in distribution are of especial interest. So far I have no information to indicate that the banded and bandless forms of *Hippodamia quinquesignata* have any differential distribution. The range of the species as a whole appears to be of some size. Leng[1] describes it as occurring from New York to California, through a northern area, but dipping to the south in the mountains of Utah, Colorado and even New Mexico. So far I have not found it in the Lower Peninsula of Michigan.

The genetic relations of the *quinquesignata* pattern to that of *convergens*, as shown by these studies, are simple enough to indicate that no large number of mutations would be required to evolve one species from the other or both from a common stock. Perhaps that is a reason why the species cross was possible. In this connection it should be stated that the cross was attempted five times. In one of these the female died several days after confinement with the male, and in another both male and female escaped in transferring them to a new culture. Thus one success in three is probably the proper measure of the ease or difficulty of making the species cross. In the two failures, mating was observed, and eggs were laid, but these did not hatch. During the copulation, the beetles were often running restlessly about, which is unusual. These facts may indicate that species crosses in nature are not likely to be frequent.

Summary

Within the species *Hippodamia quinquesignata* and in crosses between it and *H. convergens*, four principal pairs of genes affecting elytral pattern are dem-

onstrated. The spotless gene introduced from *convergens* is as effective in suppressing the spots of the usual pattern of *quinquesignata* as that of *convergens*, and it is dominant as in the latter species. It is concluded that the band across the anterior ends of the elytra is recessive to the bandless condition (two separate spots). Presence of a lateral spot behind this band is dominant over its absence. The oblique postmedian band of *quinquesignata* is regarded as recessive to the separation of the spots whose fusion makes this band.

There are some irregularities in the inheritance of three of these characters which probably require the assumption of modifying or accessory genes. In each of these three the dominance postulated is occasionally lacking or reversed. The postmedian band may almost certainly be partly produced by other genes than the one indicated above. There is strong indication that in *H. convergens* from Colorado, a nearly spotless pattern may be attained without the dominant gene called spotless.

All in all, so far as pattern is concerned, the genetic differences between *H. quinquesignata* and *H. convergens* are not very complex. Crosses between them are not very common, however, in nature.

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✦

ADDITIONAL DATA ON SEX CONTROL IN RABBITS

J. H. Quisenberry*

A SYMPOSIUM of papers on sex control, given at the annual meeting of the American Society of Animal Production, was published in the December, 1940, number of the Journal of Heredity. In that symposium the author and Mr. S. V. Chandiramani published the results of an attempt to modify the sex ratio in rats and rabbits by using lactic acid and sodium bicarbonate douches. No modification of the sex ratio was observed for the rats. The number of rabbits obtained at that time was small but the ratios appeared abnormal. Additional litters of rabbits have been obtained and the sex ratios are shown in Table I.

TABLE I. Sex Ratios Obtained from Rabbits Douched with Lactic Acid and Sodium Bicarbonate Solutions.

3% Lactic Acid			5% Sodium Bicarbonate		
♂	♀	% ♂	♂	♀	% ♂
48	45	51.6	66	55	54.5

No effects of the douches are apparent in this table. Based on the results obtained in our laboratory with small animals, douching of farm animals to modify the sex ratio seems not only a hopeless procedure, but a dangerous one as well. Introduction of the douche into the vagina of the female may result in the spread of disease unless extremely sanitary measures are used and if too strong a solution is used the fertility may be reduced.

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*Associate Professor, Genetics Dept., Texas A. and M. College, College Station, Texas.

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